

# Vocal dialect and genetic subdivisions along a geographic gradient in the orange-tufted sunbird

Kinneret Yoktan · Eli Geffen · Amiyaal Ilany ·  
Yoram Yom-Tov · Adit Naor · Noam Leader

Received: 12 September 2010 / Revised: 18 January 2011 / Accepted: 25 January 2011 / Published online: 16 February 2011  
© Springer-Verlag 2011

**Abstract** At least four hypotheses have been suggested to explain the formation and maintenance of song dialects among birds: historic processes (epiphenomenon), genetic or local adaptation, acoustic adaptation, and social adaptation. We studied spatial and temporal distribution of dialect in the orange-tufted sunbird (*Nectarinia osea*), a small nectarivorous bird that expanded its breeding range in Israel during the past 100 years from the southern part of Rift Valley to the entire country. Sunbird range expansion was concurrent with the establishment of many small settlements with an ethos of gardening, which introduced many ornithophilous plants. We recorded songs and genetically screened individual sunbirds in 29 settlements distributed across a 380 km north–south gradient along the Rift Valley. We show that dialects cluster together into geographical regions in 70% of cases, a moderate concurrence to geography. Settlement establishment date, geographical position, and genetic distance between local populations (i.e., settlements) were all poor predictors for the variance among song dialects. The specific effect of habitat was not tested because all sampled localities were similar in their physical and acoustic properties. Using a network analysis, we show that dialects seem to aggregate

into several network communities, which clustered settlement populations from several regions. Our results are best explained by either the epiphenomenon hypothesis or the social adaptation hypothesis, but at present our data cannot state unequivocally which of these hypotheses is better supported. Last, we discovered a negative association between network centrality and genetic diversity, a pattern that requires further examination in other systems.

**Keywords** Song dialects · Cultural transmission · Network centrality · Israel · *Nectarinia osea*

## Introduction

Geographical variation in vocalizations has been documented in a wide variety of songbirds (Mundinger 1982; Catchpole and Slater 2008). Song dialects may be formed in adjacent aggregations of birds, with well-defined boundaries and with different vocalization types (Rothstein and Fleischer 1987). Several authors report recent range expansions associated with changes in song structure [the brown-headed cowbird *Molothrus ater* in California (Rothstein and Fleischer 1987; Rothstein 1994) and the house finch *Carpodacus mexicanus* in the eastern USA (Pytte 1997)]. New songs may evolve by mistakes in the learning process or improvisations and a new dialect may form due to isolation between populations or by preferential copying due to behavioral consequences (e.g., Payne 1981; Petrinovich et al. 1981; Baker and Cunningham 1985). Dialects are not found in species lacking imitative learning (Podos and Warren 2007). Following Rothstein and Fleischer (1987), Podos and Warren (2007), and Catchpole and Slater (2008), we considered four common hypotheses that purport to explain the function and maintenance of dialects in birds.

---

Communicated by M. Hughes

**Electronic supplementary material** The online version of this article (doi:10.1007/s00265-011-1149-7) contains supplementary material, which is available to authorized users.

---

K. Yoktan · E. Geffen (✉) · A. Ilany · Y. Yom-Tov · A. Naor ·  
N. Leader  
Department of Zoology, Tel Aviv University,  
Tel Aviv 69978, Israel  
e-mail: geffene@post.tau.ac.il

N. Leader  
Ecology Department, Israel Nature and Parks Authority,  
Jerusalem 95463, Israel

(1) Historical processes or epiphenomenal hypothesis—local dialects are created by occasional inaccuracies in song copying and maintained merely by geographic isolation, and are at present epiphenomena with no functional link to dialect structure (Andrew 1962, Baptista 1975; King 1972; Payne 1981; Petrinovich et al. 1981). (2) Genetic or local adaptation hypothesis—dialects are maintained because they serve as population markers that local females use to identify and thus to preferentially mate with local males (Nottebohm 1969; Baker et al. 1981; MacDougall-Shackleton and MacDougall-Shackleton 2001). One possible advantage of this scenario is that genetic adaptations to the local environment might be preserved within the population (Nottebohm 1969). (3) Acoustic adaptation hypothesis—dialects arise and are maintained because the dialect vocalization transmits best through the local habitat (e.g., Morton 1975; Wiley and Richards 1978). 4. Social adaptation hypothesis - dialects are maintained through the copying of songs of established males for the purpose of gaining status, acquiring territory and mates. In order to acquire a territory and/or a mate, males must establish their status. Therefore, it is advantageous to copy a local male, one holding a territory and/or having a mate. This mechanism of dialect maintenance suggests that song learning may continue after the juvenile period if there is dispersal from the parental population (Payne 1981) or by selective song attrition (Nordby et al. 2007). Under this hypothesis, Rothstein and Fleischer (1987) define two subhypotheses: deceptive convergence and honest convergence. In our analyses, we did not attempt to distinguish between these two possibilities because the critical predictions required cannot be evaluated using our data.

Recent reviews found that none of the above hypotheses could account alone for all or even a majority of published examples of dialects (e.g., Slabbekoorn and Smith 2002a; Podos and Warren 2007). Further, most studies examining the relationship between cultural evolution (i.e., song dialect) and genetic differentiation (i.e., local adaptation hypothesis) so far have discovered limited or no degree of correlation between vocalizations and neutral genetic markers (e.g., Baker 1982; Handford and Nottebohm 1976; Loughheed and Handford 1992; Loughheed et al. 1993; Wright and Wilkinson 2001; Leader et al. 2008; Nicholls et al. 2006; Ruegg et al. 2006; Soha et al. 2004; Wright et al. 2005). These results may be due to the fact that cultural evolution can proceed at a much faster rate than neutral genetic divergence (e.g., Noad et al. 2000).

The orange-tufted or Palestine sunbird (*Nectarinia osea*; hereafter the sunbird) is a small (6–8 g) passerine that feeds on nectar, insects, spiders, and other invertebrates (Paz 1986; Cheke et al. 2001). Its range is patchy across north-central Africa, penetrating north along the Great Rift Valley on the eastern shores of the Red Sea as far as Israel (Cheke

et al. 2001). In the mid-nineteenth century, it was reported to breed in Israel only along the shores of the Dead Sea and the lower Jordan Valley (Jericho, 31°51'19.6" N, 35°27'43.85" E; Tristram 1884; Aharoni 1943/6). However, during winter (i.e., outside the breeding season), it has been reported from other (northern) parts of the country (Shirihai 1996; Cheke et al. 2001). The original breeding range of the sunbird in Israel almost overlaps that of the common hemiparasitic mistletoe, *Loranthus acaciae* (Yom-Tov and Mendelssohn 1988) whose prominent ornithophilous flowers are a favorite food source for the sunbird (Vaknin et al. 1996). The number of native ornithophilous plants available in the rest of Israel was previously very small, thus limiting nectar availability for the sunbird, and it has been suggested that the former breeding distribution of the sunbird was limited by the scarcity of ornithophilous flowers elsewhere (Smoli 1957; Paz 1986).

Since the 1930s, the sunbird has expanded its distribution to other areas, and it currently breeds throughout Israel (Shirihai 1996). The expansion of its breeding range occurred concurrently with the increase and cultural shift in the local human population. The human population increased about 15-fold and the number of settlements in Israel proper increased between 1948 and 2000 from ca. 500 to about ca. 1,200 (Statistical Abstracts of Israel 2001). Water, formerly available mostly for household consumption and to some extent also for agriculture, became available also for gardening (Enis and Ben Arav 1994). More than 1,400 plant species were introduced to Israel during the twentieth century, among them many ornithophilous ones, all of which are now very common in urban as well as agricultural settlements throughout Israel (Fahn and Zohary 1981).

The sunbird has extensive intraspecific variation in its songs, and during the breeding season individuals sing from high perches in their territories (Leader et al. 2000). Male song is highly stereotyped, and males usually sing only one song type with little or no variation throughout their lives (Leader et al. 2000). A typical song consists of four syllable types, and the last part of the song almost always consists of a trill. Sunbirds display regional vocal dialects throughout Israel, with the trill exhibiting large variability between different populations, both in frequency and temporal characteristics (Fig. 1). For example, in northern Tel Aviv, the sunbird population exhibited two distinct song dialects on a microgeographic scale (Leader et al. 2008), which divided the small, yet densely populated neighborhood into two separate areas, with a sharp boundary between them (Leader et al. 2008). Sunbird populations in other parts of Israel have their own song dialects. Dialects and geographical song variation have 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 sunbird species, *Nectarinia kilimensis* and *Nectarinia chalybeus*, as well (Grimes 1974).

We selected the orange-tufted sunbird as a model system for several reasons. The recent documented range expansion of this bird and the variety of dialects present across the Rift Valley provide a unique setup to examine the various hypotheses for dialect formation and maintenance. In our study system, the southern sunbird population presumably was the sole source of migrants that settled the northern Rift Valley during the past 100 years, and there is reliable information for most localities about the dates when new suitable habitats became available for sunbirds (Enis and Ben Arav 1994). All these novel habitats were in agricultural settlements with planted gardens, environmentally similar to each other, thus partially controlling for environmental conditions.

Considering the above background and our results, we evaluated the suitability of each of the above hypotheses as a possible explanation for the variation observed between sunbird dialects along the Rift Valley in Israel.

## Materials and methods

### Study area

The Israeli part of the Syrian–African Rift Valley ranges along ca. 400 km from Eilat in the south to Dan in the north and its width varies between 5 and 20 km. It is subdivided along a south–north axis into four sections: the Arava Valley (all locations south of latitude 31°N), the Dead Sea region (all locations between latitude 31° and 32°N), the Jordan Valley (incorporating the Bet Shean and Kinnarot valleys; all locations between latitude 32° and 33°N), and the Hula Valley (all locations north of latitude 33°N; Fig. 1). Its climate varies greatly from extreme dry (mean annual rainfall about 25 mm) and hot desert dotted with oases in the Arava and along the shores of the Dead Sea, to mild Mediterranean climate in the Hula Valley (mean annual rainfall about 550 mm).

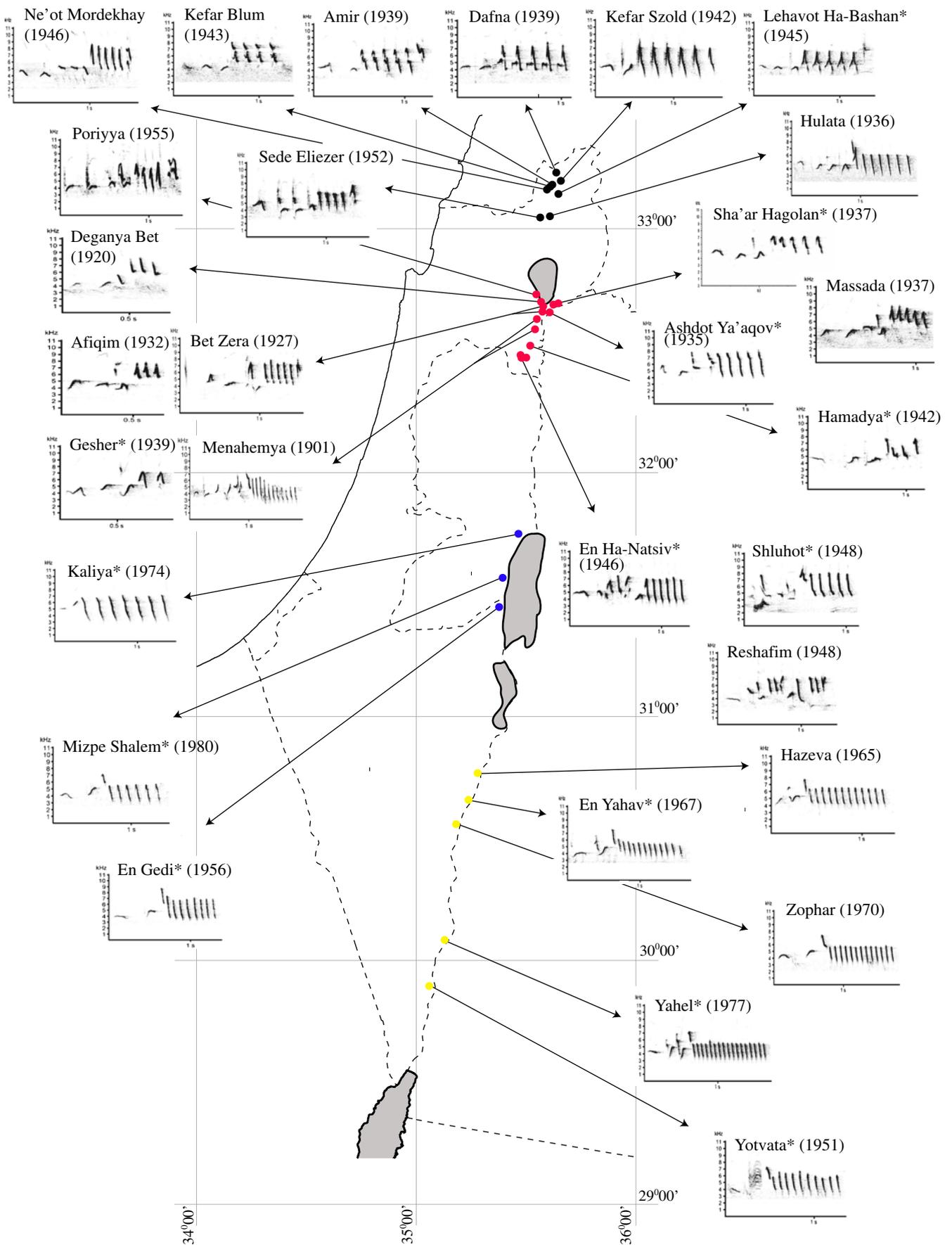
Until the beginning of the twentieth century, the sunbird was known to breed in oases along the shores of the Dead Sea and south of it, but from the 1930s on, it started to expand its distribution to other parts of Israel. There is little information about the timing of the expansion and first breeding of the sunbird in the Israeli part of the Rift Valley. The first sighting record from the Kinnarot Valley (south of the Sea of Galilee; mid-latitude 32.60°N) is from 1939 and first nests were reported in 1955 (Lulav 1969). The first nests in the Bet Shean Valley (32.50°N) and the Hula Valley (mid-latitude 33.05°N) were noted in 1955 (Inbar 1975/6) and the early 1960s (D. Eisikovitz and Y. Lev-Ari,

personal communication). We used the year of settlement establishment as a proxy for the approximate period of settlement by sunbirds (Statistical Abstracts of Israel 2001).

### Song analysis

We recorded songs from territorial male orange-tufted sunbirds inhabiting 29 collective (kibbutz) and cooperative agricultural (moshav) settlements along a 380 km latitudinal gradient in the Rift Valley (Fig. 1). We considered individuals sampled at each settlement as a population. Recordings were made during two breeding seasons (March–June 2006–2007). In order to reduce the possibility of repeated recording of the same male, most recordings within a settlement were done on the same day, and after determining the boundaries of each male territory during the previous day or two. In the few cases where we recorded in the same area at a later date, we selected territories farther away from where the previous recordings were conducted. All recordings were made within close proximity to singing birds (5–10 m) using a Sennheiser ME-67 “shotgun” microphone and a solid-state digital sound recorder (Marantz PMD670). Songs were recorded at 16-bit with a 44.1 kHz sampling rate. After transferring the digital song recordings to a computer, all song recordings were band-pass filtered from 2 to 10 kHz to eliminate environmental noise and stored as individual computer files.

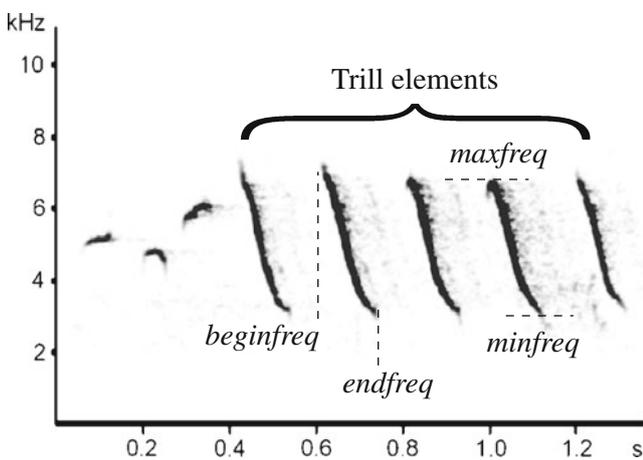
We recorded 692 songs from 141 males in 29 settlements (Fig. 1). For each male, we obtained a high quality recording of three to five songs (mean±SD of 4.9±0.03 songs per individual), taken on 1–3 consecutive days. By recording each unmarked male over a short period of time, we minimized the probability of territorial shifts and misidentification. 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). Previously, Leader et al. (2000, 2002, 2005) showed that the trill component reliably separates dialects at the microgeographic level. Therefore, in this study, we analyzed only populations that had the trill component. Songs recorded at several other localities (all in the Bet Shean Valley) completely lacked the trill component, and these were not included in our analysis. We measured the following nine trill variables from each song (Fig. 2): (1) *beginfreq*—the frequency at the beginning of the trill element (kHz), (2) *minfreq*—the lowest frequency of the trill element (kHz), (3) *endfreq*—the frequency at the end of the trill element (kHz), (4) *begmaxfreq*—the difference between *beginfreq* and the maximum frequency of the trill element (kHz), (5) *maxendfreq*—the difference between *endfreq* and the maximum frequency (*maxfreq*) of



**Fig. 1** The orange-tufted sunbird populations sampled along the Rift Valley in Israel. A typical population sonogram and the date of settlement establishment are presented. Regions are indicated by color from north to south: Hula Valley (*black*), Lake Kinneret basin (*red*), Dead Sea basin (*blue*), and Arava Valley (*yellow*). An asterisk indicates sites sampled for genetics

the trill element (kHz), (6) *bandwidth*—the difference between the minimum (*minfreq*) and maximum (*maxfreq*) frequencies of the trill element, (7) *trilllength*—time length of the trill element (s), (8) *intersyllable*—the time between consecutive trill elements (s), (9) *minmaxslope*—*bandwidth/trilllength* (kHz/s). For each trill variable, we averaged over individual the measurements obtained. The variables *minfreq* and *endfreq* ( $r_{141}=0.985$ ,  $P<0.0001$ ) and *maxendfreq* and *bandwidth* ( $r_{141}=0.983$ ,  $P<0.0001$ ) were highly correlated, thus we excluded *minfreq* and *bandwidth* from all subsequent analyses. The correlation among all other variables was much lower, ranging from 0 to 0.62 (mean $\pm$ SD,  $0.27\pm 0.20$ ), which translated to a tolerance  $>0.1$  in all variables used (the tolerance of a variable, i.e.,  $1-R^2$ , which is a measure of its co-linearity with all other independent variables in the model). Means ( $\pm$ SD) of all trill variables used per location are presented in the electronic supplement S1.

To test for correspondence between capture site of individuals and their vocal profile, we applied discriminant function analysis (DFA; e.g., McLachlan 1992). The vocal variable *beginfreq* was the only one normally distributed. All other six variables were normalized using the Box-Cox transformation. The unique contribution of each variable to the discriminatory power of the model was evaluated by partial Wilk's lambda and its associated statistics. The a priori classification probabilities were set to give equal weight for each site. Classification functions were used to calculate the posterior classification probabilities for each bird. Assignment of each bird to a site was designated by



**Fig. 2** A subset of the trill variables measured in this study (see “Materials and methods” for details)

the highest posterior probability. Leave-one-out cross-validation procedure, using a single bird from the original sample as the validation data and the remaining birds as the training data, was used for evaluating the performance of the discriminant functions (SPSS 17, SPSS Inc.). This is repeated such that each observation in the sample is used once as the validation data.

We used the squared Mahalanobis distance among settlement or region centroids, generated by DFA, as a measure of similarity in vocal profile among populations. The Mahalanobis distance is a metric adapted to handle nonspherically symmetric distributions. It is simply the distance of each song from the center of mass (settlement or region) divided by the width of the confidence ellipsoid in its direction (McLachlan 1992). It is based on correlations between trill variables and it is a useful way of determining similarity in trill profile between locations. A short Mahalanobis distance implies close resemblance between trill profiles, but not necessarily related evolutionary line. The squared Mahalanobis distance between locations was the basis for a network analysis and correlations between vocal profile and genetic distances.

We used network theory to analyze dialect connectivity between populations (i.e., settlements) of sunbirds along the Rift Valley (e.g., Proulx et al. 2005). This approach allows us to model the change in dialects from south to north and to cluster locations of closely resembled vocal profiles. We inversely transformed the squared Mahalanobis distances to convert larger distances to represent more similar vocal profiles. To eliminate weak connections, we percolated the network by finding the cutoff distance value that connects all sites into a single network (i.e., one component; Rozenfeld et al. 2008). Using shorter distance values than this cutoff value would generate several disconnected networks, whereas longer distances would add surplus and less informative connections. Thus, the percolation process brings into view the backbone structure of the network. We used randomizations to test whether the density (i.e., the number of observed ties relative to the number of possible ties) of the observed network is significantly different from the density expected in random networks (tie weight=0.5). In addition, we calculated two measures from the network, eigenvector centrality and betweenness (Wey et al. 2008, Coleing 2009). Centrality is often evaluated as the number of connections each site has with others (degree). Eigenvector centrality is an approach for finding the most central actors in a network using factor analysis. Betweenness is the number of connections between other sites that run through a given site (Freeman et al. 1991). A location can have a very few connections (low centrality), but situated on the network such that it connects between two clusters, thus having high betweenness value. Higher betweenness implies a location that is significant in bridging between

other distant sites. Finally, we used the Girvan–Newman algorithm (Girvan and Newman 2002) to define communities (clusters in a network), and modularity ( $Q$ ) to find the most fitted number of communities (Newman and Girvan 2004). Generally speaking, the larger the value of  $Q$ , the more accurate is the partition into communities, and by maximizing  $Q$  we can detect the community structure (Newman and Girvan 2004). We examined modularity for two to ten clusters, and selected the community structure associated with the highest  $Q$  value. All network calculations were done in UCINET (version 6.0; Analytic Technologies, Lexington, KY, USA).

To associate the variation in the distance matrix among population vocal dialects (i.e., squared Mahalanobis distance; dependent) with vector variables like latitude, longitude, and date of settlement establishment (independent variables), we employed the BIOENV procedure of Clarke and Ainsworth (1993). The BIOENV is a nonparametric statistical procedure that calculates the Spearman's rank correlation coefficient ( $r_s$ ) between the distances in the response distance matrix (in our case, a matrix of squared Mahalanobis distances) and a Euclidean distance matrix calculated from one or more predictor variables. Thus, the BIOENV statistic is similar to a nonparametric version of a simple Mantel's correlation between two distance matrices. The BIOENV procedure calculates the value of  $r_s$  for all possible subsets and finds the “best fit” (i.e., that combination of predictor variables whose Euclidean distance matrix yields the highest value of  $r_s$ ). Unlike  $R^2$  in multiple regression analyses, the BIOENV statistics does not necessarily increase with the increase in the number of predictor variables. A permutation test that accounts for the selection process was used for calculating the probability that the observed  $r_s$  is significantly different from no association. The BIOENV analysis was performed using the *Primer 6* computer package (Clarke and Gorley 2006).

#### Genetic analysis

We collected genetic samples from 80 individuals (69 males, six females, and five unsexed juveniles) sampled from 13 locations, which overlapped those sampled for vocalization (Fig. 1). Birds were trapped using a specially designed cone-shaped trap and a live caged male as a lure (Leader et al. 2008). Upon capture, each bird was individually ringed using numbered aluminum ring. Blood samples (~5–50  $\mu$ l) were taken in heparinized capillary tubes by means of brachial venipuncture. Samples were preserved in 1 ml of phosphate-buffered saline buffer and total cellular DNA was extracted following the protocol of Walsh (1991).

All individuals were genotyped at five polymorphic microsatellite loci using primers originally designed for the congener *Nectarinia olivacea* (R. Bowie, personal

information). All five loci were tetranucleotide repeat markers and were amplified with polymerase chain reaction (PCR) in 25- $\mu$ L volumes with a final concentration of  $1\times$  PCR buffer, 0.1 mM of each dNTP, 1–1.5 mM of  $MgCl_2$ , 0.4  $\mu$ M each of fluorescently labeled forward and unlabelled reverse primers, 2  $\mu$ L of template DNA solution, 1 unit of *Taq* polymerase, and ultrapure water to volume. PCR was performed on a Biometra TGradient Thermocycler with a profile of 95°C for 2 min, 40 cycles of 95°C for 45 s, 50–58°C for 60 s, 72°C for 120 s, and 5 min of extension at 72°C.

Products were sized on a 3,100 Genetic Analyser (Applied Biosystems) and allele sizes were scored using GeneScan software (Applied Biosystems) after calibration with an internal size standard. Positive controls (i.e., amplicons of known sequence and size) were included to ensure consistent size scoring across all runs.

We used Genepop (4.0.9; Raymond and Rousset 1995) to test for Hardy–Weinberg equilibrium and linkage disequilibrium, and FSTAT (2.9.3.2; Goudet 1995) for allelic richness and the genic diversity of Nei (1973). In the calculations of allelic richness, the program FSTAT uses rarefaction procedure to account for the difference in population sample size. We used the program Populations (1.2.28; Langella, CNRS) to calculate the following genetic distances among populations: Weir and Cockerham (1984)  $F_{st}$ , Nei et al. (1983)  $D_A$ , and Slatkin (1995) ASD. All correlations between genetic, geographic, and vocal matrices were performed using the Mantel's test.

Last, to examine whether population genetic structure can be explained by dialects we employed an assignment test, which tests for significant genetic differentiation between individuals located at different vocal communities. We used the Rannala and Mountain (1997) Bayesian algorithm for detecting migration and the probability simulation algorithm by Paetkau et al. (2004), with 1,000 simulated individuals and  $\alpha=0.01$ . These calculations are implemented in the program GENECLASS2 (Piry et al. 2004).

#### Results

The DFA indicated that the populations differed significantly in their vocal profile (for all seven vocal variables Wilks' lambda ranged 0.128–0.346,  $F_{(28,112)}\geq 7.5$ ,  $P<0.0001$ ). Out of the 406 possible pairwise comparisons between 29 populations, only eight population pairs had a squared Mahalanobis distance that was not significantly larger than expected by random ( $P<0.05$ ). Six out of the seven canonical roots had an eigenvalue  $\geq 1$ , but the first two roots accounted for approximately 75% of the variance in the data matrix (Table 1). The vocal variables *endfreq*, *trilllength*, and

**Table 1** The standardized canonical discriminant function coefficients based on population vocal profile

Trill variables	Discriminant roots						
	1	2	3	4	5	6	7
<i>beginfreq</i>	-0.212	-0.383	1.192	1.842	-0.271	-1.151	1.141
<i>endfreq</i>	0.880	-0.674	-0.570	-0.667	0.315	1.012	-0.853
<i>begmaxfreq</i>	0.156	-0.806	-0.085	1.559	-0.354	-1.088	0.184
<i>maxendfreq</i>	-0.077	0.313	-0.462	-0.209	0.306	1.174	-1.255
<i>trillength</i>	0.762	0.554	-0.057	-0.266	-0.403	0.144	0.649
<i>intersyllable</i>	0.622	0.301	0.362	0.036	0.718	-0.328	-0.089
<i>minmaxslope</i>	-0.125	0.796	-0.301	-0.424	0.679	0.263	0.907
Eigenvalue	13.5	7.3	3.0	2.1	1.3	1.0	0.7
% of variance	46.6	25.3	10.4	7.2	4.5	3.5	2.6
Cumulative %	46.6	71.9	82.2	89.5	94.0	97.4	100.0

The eigenvalue, percent of variance accounted, and the cumulative percentage of variance explained for each root are indicated at the bottom of the table

*intersyllable* were the most significant for the discrimination, as they comprised the first root that accounted for nearly 50% of the variance. We assigned equal prior probability for groups. Classification success was high: 84.4% of original grouped cases were correctly classified. Out of 29 populations, all members of 14 populations were unmistakably classified as members of their original populations (100%). In another ten populations the success rate was 80%, and only for Sde Eliezer and Yotvata was the classification rate  $\leq 40\%$ . Our DFA showed that 66.7% of cross-validated cases were correctly classified into their original population.

The above vocal variables were also effective in assigning individuals into the four geographical regions indicated in Fig. 1 (for six vocal variables Wilks' lambda ranged 0.427–0.821,  $F_{(3,137)} \geq 9.9$ ,  $P < 0.0001$ ; *minmaxslope* was insignificant). All pairwise Mahalanobis distances between region centroids were significantly larger than expected by random ( $P < 0.001$ ). Our analysis showed that 73.8% of original grouped cases were correctly classified to their original region, and the cross-validation correctly classified 70.9% of cases. Classification success in the regions of Lake Kinneret basin, Dead Sea basin, and the Arava Valley were high (76.2%, 80.0%, 91.3%, respectively). Only in the Hula Valley classification success was considerably lower (57.5%). Of the cases recorded in this region, 27.5% and 12.5% were classified as dialects from the Dead Sea basin and Lake Kinneret basin, respectively.

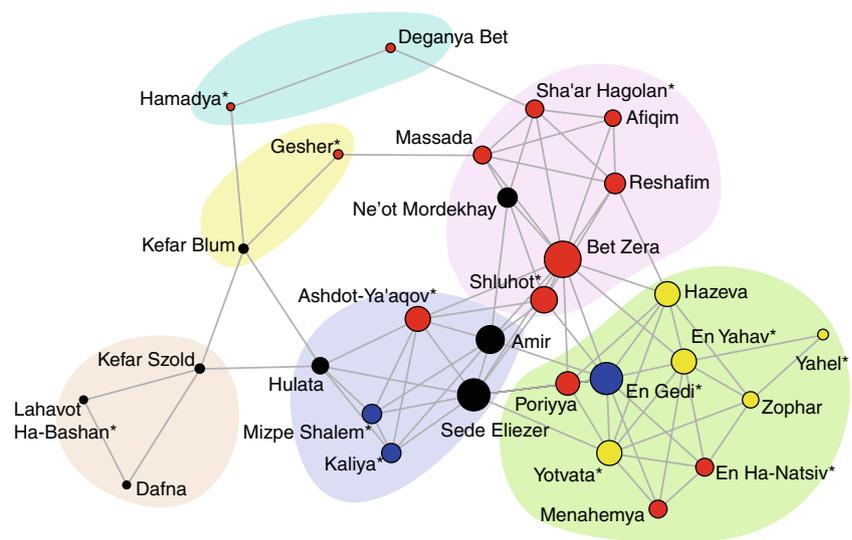
We constructed a dialect network based on the squared Mahalanobis distance between population centroids. We identified a distance value of 22 as the network percolation point (Appendix 1), thus using all the distances equal or smaller than this threshold to construct the network (Fig. 3). The network density ( $0.036 \pm 0.0016$ ), describing the density of links between locations relative to the maximum possible, was significantly lower ( $P = 0.0002$ ) than the expected in a random network. Using the Girvan and Newman (2002)

algorithm, the highest modularity ( $Q = 0.442$ ), representing the best community classification, identified six communities on the network (Fig. 3). The resulting network revealed several key properties of sunbird dialect subdivisions. First, clustering was partially associated with geography. The largest community included all the localities from the Arava Valley, the second largest community was from the Lake Kinneret basin where nearly all locations from this region were included, and two of the smaller communities (two to three locations) each composed from localities of the same region (Fig. 3). However, two other communities had a mix of localities from three different regions (Fig. 3). Second, the most central populations in this network were Sde Eliezer, Bet Zera, and En Gedi, each of which was located within a different network community and geographic region (Figs. 1 and 3). Three of the locations in the Arava were of high centrality, and most of the outermost northern locations (Hula Valley) were of low centrality (Fig. 3). Last, in this network, betweenness was completely independent of centrality ( $r_s = -0.008$ ,  $P = 0.965$ ), suggesting that high centrality populations are not necessarily bridging between network communities. The top betweenness populations were Kefar Blum, Kefar Szold, Hulata, and Sha'ar Hagolan, which bridged between the northernmost locations and all other locations.

Using the BIOENV analysis, we found that latitude and settlement establishment dates were the best predictors for the distances among dialects (Table 2). However, even the best variable subset (i.e., latitude and establishment date) accounted for only 9.9% of the variance in dialects, and latitude alone accounted for only 4.4% (Table 2).

The five microsatellite loci used in this study were highly variable (Table 3) and completely independent (linkage disequilibrium;  $P \geq 0.495$  in all comparisons). We did not detect overall significant heterozygote deficiency ( $P = 0.571$ ) or excess ( $P = 0.419$ ) and this trend also held for each population when tested separately (all  $P$  values  $> 0.05$ ),

**Fig. 3** Song dialects network based on the squared Mahalanobis distance between population centroids. Color denotes region assignment and symbol size is proportional to eigenvector centrality. Regions are shown left to right from north to south: Hula Valley (black), Lake Kinneret basin (red), Dead Sea basin (blue), and Arava Valley (yellow). Color-shaded areas denotes the six communities (modularity  $Q=0.442$ ) identified by the Girvan and Newman (2002) algorithm. An asterisk indicates sites sampled for genetics



except for heterozygote deficiency in the population of Kaliya ( $P=0.008$ ).

In contrast to the dialect distribution, the genetic structure was much better predicted by geography. We detected a significant correlation between geographic distance and  $F_{st}$  (Mantel's test;  $r=0.419$ ,  $P=0.007$ ),  $D_A$  ( $r=0.617$ ,  $P=0.0001$ ; Fig. 4a), and ASD ( $r=-0.401$ ,  $P=0.01$ ). However, the genetic distances were poor predictors of dialect subdivision. Only  $D_A$  significantly correlated with squared Mahalanobis distance (Mantel's test;  $r=0.289$ ,  $P=0.004$ ; Fig. 4b), and that relationship accounted only for about 8% of the variance.  $F_{st}$  ( $r=-0.047$ ,  $P=0.699$ ) and ASD ( $r=-0.017$ ,  $P=0.885$ ) were independent of the squared Mahalanobis distance. After controlling for the effect of geographic distance, none of the genetic distances was significantly associated with the squared Mahalanobis distance ( $D_A$ ,  $r=0.128$ ,  $P=0.243$ ;  $F_{st}$ ,  $r=-0.188$ ,  $P=0.118$ ; ASD,  $r=0.114$ ,  $P=0.305$ ). In addition, only 32.1% of individuals were correctly assigned to their vocal community based on their genetic profile and the Bayesian procedure in GENECLASS2.

**Table 2** The BIOENV correlation analysis between the matrix of population vocal distances and latitude, longitude and year of settlement establishment

Variable set	$r_s$	$P$
Latitude, year	0.314	0.0008
Latitude, longitude, year	0.308	0.0008
Longitude, year	0.303	0.0011
Longitude	0.269	0.0015
Latitude, longitude	0.251	0.0071
Year	0.239	0.0101
Latitude	0.222	0.0169

All possible subsets and their associated statistics are presented, and sorted by their  $r_s$  value

Last, we examined whether genetic variability at each site, a reflection of dispersal, is associated with vocal connectivity (e.g., network centrality). We found that genetic variability significantly correlated with the dialect eigenvector centrality (allelic richness,  $r_s=-0.621$ ,  $P=0.024$ ; gene diversity,  $r_s=-0.725$ ,  $P=0.005$ ; Fig. 4c), but not with dialect betweenness (allelic richness,  $r_s=-0.297$ ,  $P=0.324$ ; gene diversity,  $r_s=-0.421$ ,  $P=0.152$ ). The negative association between genetic variability and eigenvector centrality was significant even after exclusion of the population with the highest centrality value (allelic richness,  $r_s=-0.539$ ,  $P=0.058$ ; gene diversity,  $r_s=-0.665$ ,  $P=0.013$ ).

## Discussion

Geographical dialects have been documented in a wide variety of avian species, mainly in oscine songbirds (Mundinger 1982). Song dialects are thought to be a product of cultural evolution, whereby geographic variation is maintained through the preferential learning of local variants (reviewed in Catchpole and Slater 2008). Four hypotheses were advanced to purport the creation and maintenance of dialects, and below we discuss the consistency of each with our results on the sunbird along the Rift Valley.

*Hypothesis 1 (historical processes or epiphenomena)* Colonization of new areas by songbirds is thought to be one process through which regional differences in song may arise (Baker and Cunningham 1985). However, only in a very few species showing geographic dialects has the historical process of dialect formation been determined. Such an example is the concurrent change in the whistle structure of the brown-headed cowbird (*M. ater*) following

**Table 3** Sample size ( $n$ ), mean alleles number ( $N_{\text{Alleles}} \pm \text{SD}$ ), allelic diversity (AD; adjusted for the minimal sample size of 2), mean Nei's genic diversity ( $\pm \text{SD}$ ), and observed and expected heterozygosity ( $H_o$  and  $H_e$ ) for 13 populations

Population	$n$	$N_{\text{Alleles}}$	AD	Nei's genic diversity	$H_o$	$H_e$
Ashdot Ya'aqov	5	5.8±1.10	3.2	0.86±0.06	0.820	0.767
En Gedi	17	7.6±0.89	3.0	0.79±0.06	0.830	0.766
En Ha-Natsiv	3	3.8±0.84	3.0	0.80±0.13	0.867	0.667
En Yahav	5	5.0±1.23	3.0	0.79±0.11	0.840	0.712
Gesher	4	5.4±1.52	3.3	0.88±0.08	0.950	0.769
Hamadya	6	5.4±0.55	3.0	0.82±0.02	0.867	0.750
Kaliya	4	4.2±1.10	2.9	0.76±0.10	0.550	0.669
Lehavot Ha-Bashan	9	5.4±0.89	3.0	0.81±0.03	0.867	0.763
Mizpe Shalem	8	6.2±1.48	3.1	0.83±0.03	0.707	0.776
Sha'ar Hagolan	6	4.6±0.89	2.6	0.70±0.06	0.767	0.639
Shluhot	6	4.4±1.34	2.9	0.78±0.10	0.833	0.711
Yahel	2	3.2±0.84	3.2	0.83±0.20	0.700	0.625
Yotvata	5	4.6±1.34	2.9	0.78±0.11	0.730	0.700

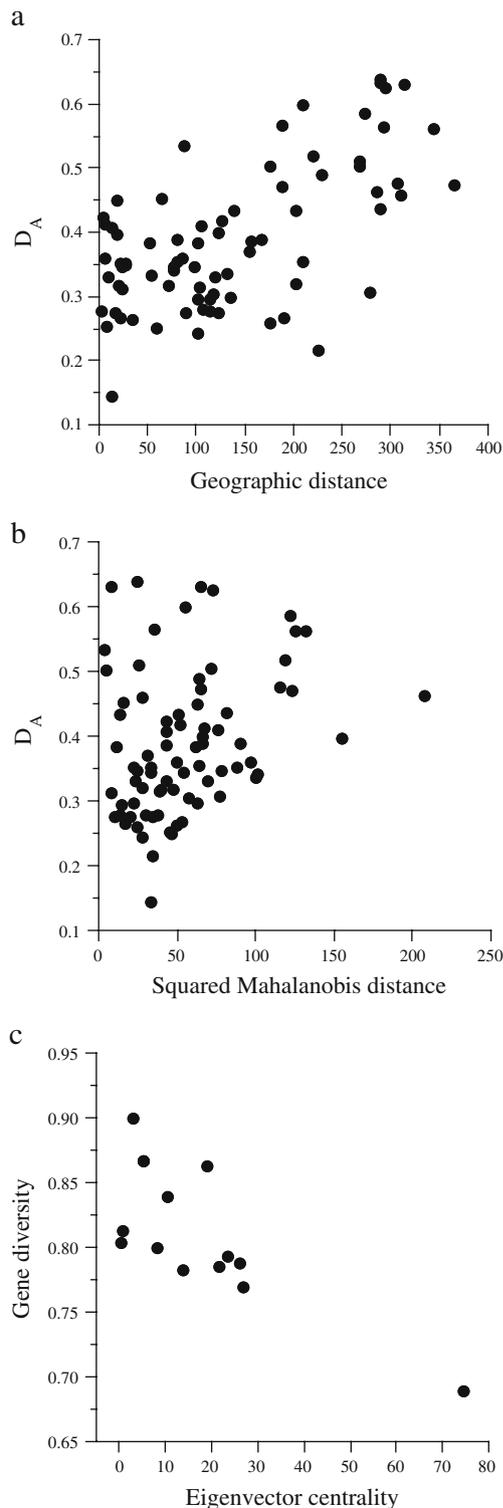
Larger values indicate higher genetic diversity

its recent range expansion in California (Rothstein and Fleischer 1987; Rothstein 1994). The occurrence of distinct dialects on a macrogeographic scale in the song of the sunbird along the Rift Valley in Israel is therefore not surprising, as most populations of sunbirds are sedentary and are isolated from one another by large areas of unsuitable habitat, particularly in the Arava Valley. Although, breeding sunbirds are often faithful to their territories (Zilberman et al. 2001), during the nonbreeding season they are also local wanderers and short-distance migrants (Shirihai 1996; Cheke et al. 2001). Hence, the observations before the beginning of the early 1900s that spotted sunbirds outside their southern breeding distribution range mostly during winter (reviewed by Shirihai 1996). Thus, sunbird capability of long distance flights, and that vocal communities composed of locations from different regions, negates the notion that dialects formed only due to isolation.

In the case of sunbirds in Israel, history may have played a role in the formation of dialect clusters (Fig. 3). We showed that year of settlement establishment alone explained only 6%, and combined with geographical information, only 10% of the trill variation is explained (Table 3), which suggests that dialects are not formed in a gradual manner over time and space. This result should be taken with caution because of two reasons. First, there is only sketchy information about the exact sunbird establishment date (i.e., first breeding) in many localities along the Israeli Rift Valley. The existing records suggest that the temporal order of sunbird colonization followed that of modern human settlement along the Rift Valley. These records suggest that the first sunbird settlement most probably occurred in Kinnarot Valley, followed shortly after that by the Bet Shean Valley to the south of it, while the Hula Valley to the north was settled last. Although this anecdotal data appears to support the contention that

sunbird settlement in many parts of Israel is dependent on nectar-producing ornamental bushes and trees planted in gardens during the last 50 years (Enis and Ben Arav 1994), the use of settlement establishment date may not reflect correctly, in some cases, the arrival time of sunbirds. This is probably due to the fact that establishment date did not coincide with the date of water availability for gardening. Second, song types within a population may drift with time (e.g., Payne et al. 1981; Gibbs 1990). Although copying in general may be very accurate, errors may create new song types. Likewise, some song types are not copied and go locally extinct. Over 50–100 years the distribution of dialects may have been changed considerably, to a point that time can only modestly explain the contemporary dialect distribution. Thus, founder effects followed by drift may predict similar trill profiles within localities.

*Hypothesis 2 (genetic adaptation)* According to the genetic adaptation hypothesis, dialects facilitate assortative mating (Baker et al. 1986; Nottebohm 1969). Song learning provides the substrate for geographical vocal variation. Theoretically, the initial events leading to increased genetic polymorphism in a population, and eventually to speciation, need not be genetically encoded (Vaneechoutte 1997). Such events can be solely caused by phenotypic behavior, not encoded by genes, or in other words by cultural-related activity. However, it is reasonable to assume that, given time, genetic differentiation will be created between separate populations. We found that genetic structure was strongly predicted by geography, which may suggest a pattern of isolation by distance. However, genetic proximity did not reflect on the distance between dialects (Table 4). The former result would be expected if sunbirds most often breed locally, and if those that disperse often end up as unsuccessful breeders. On the other hand, the lack of correlation between dialect and genetic distances supports



**Fig. 4** Genetics as a predictor in dialect subdivision: **a** the correlation between Nei's  $D_A$  genetic distance and geographic distance (Mantel's test;  $r=0.617$ ,  $P=0.0001$ ); **b** the correlation between Nei's  $D_A$  genetic distance, and population dialect squared Mahalanobis distance (Mantel's test;  $r=0.289$ ,  $P=0.042$ ); and **c** the correlation between Nei's gene diversity and dialect network eigenvector centrality ( $r_s=-0.725$ ,  $P=0.005$ )

the idea that songs are locally learned by dispersers and individuals are not fixed on their parent's dialect (e.g., social adaptation hypothesis) or it is a result of vocal drift. This result can also be explained by the theory of selective attrition, where young songbirds memorize many songs in their natal range, but use only a few in their final repertoire. Under this theory, dispersers may keep the song(s) that match most neighbors in their new surrounding and drop the rest (Nordby et al. 2007).

Further, our finding that genetic variability is inversely correlated with dialect centrality suggests a more complex pattern. High centrality populations can be viewed as dialect distributors, i.e., the origin population of a successful dialect. We assume that dialect-distributing populations are well established and thus provide little room for outsiders to infiltrate and become successful breeders. This assumption is supported by the fact that most locations with high centrality also showed high classification success in the DFA (only Yotvata and Sde Eliezer were exceptions), and further by our finding that centrality and betweenness were not correlated, which suggests that locations of high centrality are not bridging between distant populations. In contrast, low centrality populations are probably those that are less stable, a situation that permits establishment by migrants. The above scenario would result in higher genetic variability in low centrality populations. The alternative view that high centrality populations are sinks has little support in our case because such a scenario would suggest higher genetic variability in locations with high network centrality.

Our study adds to the growing number of studies that have used sensitive, rapidly evolving genetic markers, such as microsatellites (e.g., Leader et al. 2008; Nicholls et al. 2006; Ruegg et al. 2006; Soha et al. 2004; Wright et al. 2005), yet fail to find a direct association between song and genetic variation in dialect species. This is contrary to predictions of the long-standing hypothesis that avian dialects contribute to reproductive isolation between populations (but see MacDougall-Shackleton and MacDougall-Shackleton 2001 for correlation between dialect and genetic distances). The lack of correspondence between genetics and dialects could have arisen from a lack in genetic variability. However, this seems highly unlikely in our case because the microsatellite markers we used were highly polymorphic (Table 3) and generated a clear genetic pattern on the geographical scale, but not on the dialect scale.

**Hypothesis 3 (acoustic adaptation)** Several recent studies have discovered a significant correlation between ecological and acoustic distance after accounting for genetic distance (Nicholls et al. 2006; Ruegg et al. 2006), suggesting a potential role for ecological selection on divergence in spectral and temporal components of bird song. According

**Table 4** The four hypotheses considered in this study to explain maintenance of dialects in sunbirds

Hypothesis	Predictions	This study
Historical processes or epiphenomenal	Nearby settlements established at the same period of time are occupied by sunbirds with a similar trill profile	Supported
Genetic adaptation	Locations that show high similarity in their trill profile are occupied by genetically related individuals	Weakly supported
Acoustic adaptation	Locations that are physically similar in their acoustic properties show similarity in their trill profile	Not directly tested. All localities were presumed to be acoustically structurally similar
Social adaptation	A similar trill profile is observed within localities. Neighboring localities may have different dialects. Birds singing the same dialect are not necessarily genetically or socially related	Supported, however, the exact mechanism of social benefits that may be acquired has yet to be determined

to Nicholls et al. (2006), divergence in vocalizations among genetically related populations in different habitats suggests that dialect species match their vocalizations to the environment in which they live, despite the homogenizing influence of gene flow. In combination with convergence of vocalizations among genetically divergent populations occurring in the same habitat, this shows the overriding importance that habitat-related selection can have on the establishment and maintenance of variation in vocalizations.

In this context, our findings of the existence of distinct vocal dialects in the sunbird do not appear to strictly represent habitat-induced selection. This was previously shown on a microgeographic scale in Israel (Leader et al. 2005; Leader et al. 2008) and now on a macrogeographic scale (this study). We showed that the vocal communities identified by the Girvan–Newman algorithm (Fig. 3) clustered locations from several radically different climate zones. The 29 sunbird populations sampled for this study were situated within a 380 km latitudinal and climate gradient along the Israeli Rift Valley, and represent diverse natural habitat types, caused by environmental conditions. However, as the study focused on birds inhabiting human settlements along this gradient, one must regard the strong anthropogenic effect imposed on the natural habitat. The availability of water for gardening has rapidly transformed these settlements into “green islands”, supporting not only a large number of ornithophilous plant species appealing to sunbirds, but also green lawns and many species of trees planted for shade and recreation purposes. Thus, despite the geographic distance and the extreme variability in the surrounding natural habitat and environmental conditions, these settlements are not only essentially similar in composition and abundance of food resources available for sunbirds, they are also similar in the acoustic constraints they impose on the local habitat. The predominant selection pressures that may modify the structure of long-distance acoustic signals, so as to maximize their transmission, are (1) the “habitat matching” hypothesis (Hansen 1979) that sound transmission properties are associated with local

microclimate and vegetation structure (Wiley and Richards 1978, Brown and Handford 2000, Slabbekoorn et al. 2002) and (2) signal interference by local ambient noise patterns (Brenowitz 1982, Ryan and Brenowitz 1985, Nelson and Marler 1989, Slabbekoorn and Smith 2002b, Slabbekoorn and Peet 2003). We argue that most of the settlements we sampled are similar in their human lifestyle, landscape design, and resulting gardening practices, causing a homogenizing effect on the acoustic properties of the local habitat (in terms of both sound transmission properties and ambient noise patterns). The result of any ecological selection on divergence in sunbird song should therefore translate into a homogenizing effect on song dialects as well. Although we have not directly tested for environmental effects on dialect pattern, the fact that all sunbirds were sampled in comparable human habitation and dialects were only partially clustered by regions provide little support for this hypothesis (but see Table 4).

*Hypothesis 4 (social adaptation; deceptive or honest convergence)* Our data show that sunbird dialect distribution corresponds to geography. Dialects seem to aggregate around several settlements that form dialect centers (Fig. 3). The most central populations in our study were Bet Zera, Sde Eliezer, and En Gedi, located in the Kinnarot Valley, Hula Valley, and the Dead Sea area, respectively. Further, our DFA successfully assigned about 84% of individuals back to their capture sites based on their vocal profile, a result indicating high vocal uniformity within sites. The above spatial pattern of dialect distribution conforms to the social adaptation hypothesis in which dialects are maintained through the copying of songs of established males (Table 4). These results also suggest that song learning may continue after the juvenile period if there is dispersal from the parental population or by selective song attrition. Support for the social adaptation hypothesis also comes from a study of urban population of the orange-tufted sunbird, where confounding effects of isolation, history or acoustic adaptations are not relevant (Leader et al. 2008).

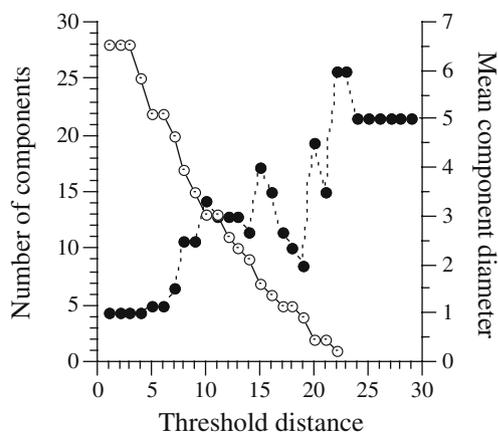
Nevertheless, unrecorded drift in song types over time and founder effects cannot be excluded as an alternative mechanism (the epiphenomenal hypothesis) given our current data.

In conclusion, our results are best explained by either the epiphenomenon hypothesis or the social adaptation hypothesis, but at present our data cannot state unequivocally which of these hypotheses is better supported. The genetic adaptation hypothesis conforms considerably less to our data (Tables 2 and 4). The acoustic adaptation was not directly tested but the physical and vegetational uniformity of our sites and the clusters of locations from several radically different habitats may suggest weak support for this hypothesis. These interpretations are in the same line suggested by earlier studies on sunbird dialects (Leader et al. 2000, 2008). Last, the association between dialect centrality and genetic variation is intriguing because it reflects on the how dispersers establish themselves in target populations, and requires examination in other systems.

**Acknowledgments** We are grateful to Dini Eisikovitz, Yossi Lev-Ari, and Uzi Paz for unpublished information and advice; to Stephen I. Rothstein, Jonathan Wright, and Shai Markman for their constructive comments; and to Naomi Paz for editing the article. We acknowledge useful suggestions and constructive criticism provided by Melissa Hughes and three anonymous reviewers. This research was supported by The Israel Science Foundation (grant no. 900/04) to YYT and by the Israel Cohen Chair for Environmental Zoology to YYT.

## Appendix 1

Number of components (i.e., a component is a set of connected populations) and mean component diameter as a function of squared Mahalanobis distance threshold value. The network percolation point is defined as the threshold squared Mahalanobis value where number of components equals one (i.e., single network with all populations connected) and the mean component diameter is maximal.



## References

- Aharoni I (1943/6) Memories of a zoologist. Am Oved, Tel Aviv. In Hebrew.
- Andrew RJ (1962) Evolution of intelligence and vocal mimicking. *Science* 137:585–589
- Baker MC (1982) Vocal dialect recognition and population genetic consequences. *Am Zool* 22:561–569
- Baker MC, Cunningham M (1985) The biology of bird-song dialects. *Behav Brain Sci* 8:85–133
- Baker MC, Spitzer-Nabors KJ, Bradley DC (1981) Early experience determines song dialect responsiveness of female sparrows. *Science* 214:819–820
- Baker MC, Bierke TK, Lampe H, Espmark Y (1986) Sexual response of female great tits to variation in size of male's song repertoires. *Am Nat* 128:491–498
- Baptista LF (1975) Song dialects and demes in sedentary populations of the white-crowned sparrow (*Zonotrichia leucophrys nuttalli*). *Publ Zool Univ Calif* 105:1–52
- Brenowitz EA (1982) Long-range communication of species identity by song in the red-winged blackbird. *Behav Ecol Sociobiol* 10:29–38
- Brown TJ, Handford P (2000) Sound design for vocalizations: quality in the woods, consistency in the fields. *Condor* 102:81–92
- Catchpole CK, Slater PJB (2008) Bird song: biological themes and variations. Cambridge University Press, Cambridge
- Cheke RA, Mann CF, Allen R (2001) Sunbirds. Yale University Press, New Haven
- Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. *Mar Ecol Prog Ser* 92:205–219
- Clarke KR, Gorley RH (2006) PRIMER v6: user manual/tutorial. Primer-e, Plymouth
- Coleing A (2009) The application of social network theory to animal behaviour. *Biosci Horiz* 2:32–43
- Enis R, Ben Arav Y (1994) Gardens and landscape in the kibbutz: 60 years of development (1910–1970). Ministry of Defense Publishing House, Tel Aviv, In Hebrew
- Fahn A, Zohary M (1981) The cultivated plants of Israel. Hakibbutz Hameuchad, Tel Aviv, In Hebrew
- Freeman LC, Borgatti SP, White DR (1991) Centrality in valued graphs: a measure of betweenness based on network flow. *Soc Networks* 13:141–154
- Gibbs HL (1990) Cultural evolution of male song types in Darwin's medium ground finch *Geospiza fortis*. *Anim Behav* 39:253–263
- Girvan M, Newman MEJ (2002) Community structure in social and biological networks. *Proc Natl Acad Sci USA* 99:7821–7826
- Goudet J (1995) FSTAT (vers. 1.2): a computer program to calculate *F*-statistics. *J Hered* 86:485–486
- Grimes LG (1974) Dialects and geographical variation in the song of the splendid sunbird *Nectarinia coccinigaster*. *Ibis* 116:314–329
- Handford P, Nottebohm F (1976) Allozymic and morphological variation in population samples of rufous-collared sparrow, *Zonotrichia capensis*, in relation to vocal dialects. *Evolution* 30:802–817
- Hansen P (1979) Vocal learning: its role in adapting sound structures to long-distance propagation and a hypothesis on its evolution. *Anim Behav* 27:1270–1271
- Inbar R (1975/6) The birds of Eretz Israel. Yavneh, Tel Aviv, In Hebrew
- King JR (1972) Variation in the song of the rufous collared sparrow, *Zonotrichia capensis*, in northwestern Argentina. *Z Tierpsychol* 30:344–373
- Leader N, Wright J, Yom-Tov Y (2000) Microgeographic song dialects in the orange-tufted sunbird (*Nectarinia osea*). *Behaviour* 137:1613–1627

- Leader N, Wright J, Yom-Tov Y (2002) Dialect discrimination by male orange-tufted sunbirds (*Nectarinia osea*): reactions to own and neighboring dialects. *Ethology* 108:367–376
- Leader N, Wright J, Yom-Tov Y (2005) Acoustic properties of two urban song dialects in the orange-tufted sunbird (*Nectarinia osea*). *Auk* 122:231–245
- Leader N, Geffen E, Mokady O, Yom-Tov Y (2008) Song dialects do not restrict gene flow in an urban population of the orange-tufted sunbird *Nectarinia osea*. *Behav Ecol Sociobiol* 62:1299–1305
- Lougheed SC, Handford P (1992) Vocal dialects and the structure of geographic variation in morphological and allozymic characters in the rufous-collared sparrow, *Zonotrichia capensis*. *Evolution* 46:1443–1456
- Lougheed SC, Handford P, Baker AJ (1993) Mitochondrial-DNA hyperdiversity and vocal dialects in a subspecies transition of the rufous-collared sparrow. *Condor* 95:889–895
- Lulav S (1969) In: Kroodsma DE, Miller EH (eds) *The population mimetics of birdsong. Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, pp 181–197
- MacDougall-Shackleton EA, MacDougall-Shackleton SA (2001) Cultural and genetic evolution in mountain white-crowned sparrows: song dialects are associated with population structure. *Evolution* 55:2568–2575
- McLachlan GJ (1992) *Discriminant analysis and statistical pattern recognition*. Wiley Interscience
- Morton ES (1975) Ecological sources of selection on avian sounds. *Am Nat* 109:17–34
- Mundinger PC (1982) In: Kroodsma DE, Miller EH (eds) *Microgeographic and macrogeographic variation in the acquired vocalizations of birds. Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, pp 147–208
- Nei M (1973) Analysis of gene diversity in subdivided populations. *Proc Natl Acad Sci USA* 70:3321–3323
- Nei M, Tajima F, Tateno Y (1983) Accuracy of estimated phylogenetic trees from molecular data. *J Mol Evol* 19:153–170
- Newman MEJ, Girvan M (2004) Finding and evaluating community structure in networks. *Phys Rev* 69:026113
- Nelson DA, Marler P (1989) Categorical perception of a natural stimulus continuum—birdsong. *Science* 244:976–978
- Nicholls JA, Austin JJ, Moritz C, Goldizen AW (2006) Genetic population structure and call variation in a passerine bird, the satin bowerbird, *Ptilonorhynchus violaceus*. *Evolution* 60:1279–1290
- Noad MJ, Cato DH, Bryden MM, Jenner MN, Jenner KCS (2000) Cultural revolution in whale songs. *Nature* 408:537–537
- Nordby JC, Campbell ES, Beecher MD (2007) Selective attrition and individual song repertoire development in song sparrows. *Anim Behav* 74:1413–1418
- Nottebohm F (1969) The song of the chingolo (*Zonotrichia capensis*) in Argentina: description and evaluation of a system of dialects. *Condor* 71:299–315
- Paetkau D, Slade R, Burden M, Estoup A (2004) Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Mol Ecol* 13:55–65
- Payne RB (1978) Microgeographic variation in songs of the splendid sunbird *Nectarinia coccinigaster*: population phenetics, habitats, and song dialects. *Behaviour* 65:282–308
- Payne RB (1981) Song learning and social interactions in Indigo Buntings. *Anim Behav* 29:688–697
- Payne RB, Thompson WL, Fiala KT, Sweany LL (1981) Local song traditions in indigo buntings: cultural transmissions of behavior patterns across generations. *Behaviour* 77:199–221
- Paz U (1986) *Birds*. Vol. 6. In: Alon A (ed) *Plants and animals of the land of Israel*. Ministry of Defence and SPNI, Israel, In Hebrew
- Petrinovich L, Patterson TL, Baptista LF (1981) Song dialects as barriers to dispersal: a reevaluation. *Evolution* 35:180–188
- Piry S, Alapetite A, Cornuet J-M, Paetkau D, Baudouin L, Estoup A (2004) GENECLASS2: a software for genetic assignment and first generation migrants detection. *J Hered* 95:536–539
- Podos J, Warren PS (2007) The evolution of geographic variation in birdsong. *Adv Study Behav* 37:403–458
- Proulx SR, Promislow DEL, Phillips PC (2005) Network thinking in ecology and evolution. *TREE* 20:345–353
- Pytte CL (1997) Song organization of house finches at the edge of an expanding range. *Condor* 99:942–954
- Rannala B, Mountain JL (1997) Detecting immigration by using multilocus genotypes. *Proc Natl Acad Sci USA* 94:9197–9201
- Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *J Hered* 86:248–249
- Rothstein SI (1994) The cowbird's invasion of the far west: history, causes and consequences experienced by host species. *Stud Avian Biol* 15:301–315
- Rothstein SI, Fleischer RC (1987) Vocal dialects and their possible relation to honest status signalling in the brown-headed cowbird. *Condor* 89:1–23
- Rozenfeld AF, Arnaud-Haond S, Hernandez-Garcia E, Eguluz VM, Serrao EA, Duarte CM (2008) Network analysis identifies weak and strong links in a metapopulation system. *Proc Natl Acad Sci USA* 105:18824–18829
- Ruegg K, Slabbekoom H, Clegg S, Smith TB (2006) Divergence in mating signals correlates with ecological variation in the migratory songbird, Swainson's thrush (*Catharus ustulatus*). *Mol Ecol* 15:3147–3156
- Ryan MJ, Brenowitz EA (1985) The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am Nat* 126:87–100
- Shirihai H (1996) *The birds of Israel*. Academic, London
- Slabbekoom H, Smith TB (2002a) Bird song, ecology, and speciation. *Phil Trans Roy Soc Lond B* 357:493–503
- Slabbekoom H, Smith TB (2002b) Habitat-dependent song divergence in the little greenbull; an analysis of environmental selection pressures on acoustic signals. *Evolution* 56:1849–1858
- Slabbekoom H, Peet M (2003) Birds sing at a higher pitch in urban noise—great tits hit the high notes to ensure that their mating calls are heard above the city's din. *Nature* 424:267
- Slabbekoom H, Ellers J, Smith TB (2002) Birdsong and sound transmission: the benefits of reverberations. *Condor* 104:564–573
- Slatkin M (1995) A measure of population subdivision based on microsatellite allele frequency. *Genetics* 139:457–462
- Smoli E (1957) *Birds in Israel*. Massada, Tel Aviv. In Hebrew
- Soha JA, Nelson DA, Parker PG (2004) Genetic analysis of song dialect populations in Puget Sound white-crowned sparrows. *Behav Ecol* 15:636–646
- Statistical Abstracts of Israel (2001) No. 52. Central Bureau of Statistics, Jerusalem
- Tristram HB (1884) *Fauna and flora of Palestine*. Palestine Exploration Fund, London
- Vaknin Y, Yom-Tov Y, Eisikovitch D (1996) Flowering seasonality and flower characteristics of *Loranthus acaciae* Zucc. (Lorantaceae): implications for advertisement and bird-pollination. *Sex Plant Repro* 9:279–285
- Vanechoutte M (1997) Bird song as a possible cultural mechanism for speciation. *J Memetics Evol Models Inform Transm* 1
- Walsh PS (1991) CHELEX-100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *Biotechniques* 10:506–513
- Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population structure. *Evolution* 38:1358–1370

- Wey T, Blumstein DT, Shen W, Jordan F (2008) Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim Behav* 75:333–344
- Wiley RH, Richards DG (1978) Physical constraints on acoustic communication in atmosphere—implications for evolution of animal vocalizations. *Behav Ecol Sociobiol* 3:69–94
- Wright TF, Wilkinson GS (2001) Population genetic structure and vocal dialects in an Amazon parrot. *Proc Royal Soc Lond B* 268:609–616
- Wright TF, Rodriguez AM, Fleischer RC (2005) Vocal dialects, sex-biased dispersal, and microsatellite population structure in the parrot *Amazona auropalliata*. *Mol Ecol* 14:1197–1205
- Yom-Tov Y, Mendelssohn H (1988) Changes in the distribution and abundance of vertebrates in Israel during the 20<sup>th</sup> century. In: Yom-Tov Y, Tchernov E (eds) *The zoogeography of Israel*. Dr. W. Junk, Dordrecht, pp 515–547
- Zilberman R, Moav B, Yom-Tov Y (2001) Territoriality and mate guarding in the Orange-tufted Sunbird. *Israel J Zool* 47:275–286