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GEOGRAPHIC PATTERNS OF SONG SIMILARITY IN THE DICKCISSEL (*SPIZA AMERICANA*)

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Abstract.—Song sharing among neighboring males is a well-known, frequent outcome of song learning in oscine passerines and some other groups, but only limited investigations of the spatial scale of this phenomenon have been pursued. On the basis of recordings of 1,043 individuals, we investigated song sharing in Dickcissels (*Spiza americana*) at local and regional scales at sites from northern Kansas to northern Oklahoma. Classification of song elements revealed decreasing song similarity with increasing distances between individual birds at small to intermediate scales, to ~10 km. At the largest spatial scales (10–300 km between sites), there was very little similarity among sites and no obvious tendency for a decrease in similarity with increasing distances among our 30 sites. At our intensively sampled site, analyses of quantitative measurements showed that, at least for our most widely shared song element, frequency and duration were more similar in closer birds. Thus, distance between birds influences both quantitative and qualitative song similarity in Dickcissels. Variability existed among sites in the shape of the song-sharing decay curve, which indicates that other factors besides distance also govern song-sharing patterns. We found high repeatability of individual songs for both second-year (SY) and after-second-year (ASY) males throughout the season, and high conformity to the local song neighborhood in both SY and ASY males from their first recording soon after arrival in May. Returning ASY males sang the same song they had produced the previous breeding season. *Received 4 October 2007, accepted 7 June 2008.*

Key words: culture, dialect, Dickcissel, Passeriformes, song sharing, spatial scale, *Spiza americana*.

Patrones Geográficos en la Similitud del Canto en *Spiza americana*

Resumen.—La similitud del canto entre machos vecinos es un resultado conocido y frecuente del aprendizaje del canto en los paseriformes oscinos y en algunos otros grupos. Sin embargo, un escaso número de estudios han investigado la escala espacial de este fenómeno. Con base en grabaciones de 1043 individuos, investigamos la similitud del canto en *Spiza americana* a una escala local y regional en sitios ubicados desde el norte de Kansas hasta el norte de Oklahoma. La clasificación de los elementos del canto reveló una similitud decreciente con el aumento de la distancia entre individuos a escalas pequeñas e intermedias hasta ~10 km. A la escala espacial mayor (10–300 km entre sitios), hubo muy baja similitud entre sitios, y no existió una tendencia obvia de disminución de la similitud con el aumento de la distancia entre nuestros 30 sitios. En nuestro sitio intensamente muestreado, los análisis de mediciones cuantitativas mostraron que, por lo menos para los elementos del canto que son ampliamente compartidos, la frecuencia y la duración fueron más similares entre aves más cercanas. Así, la distancia entre las aves influenció tanto la similitud cuantitativa como la similitud cualitativa del canto en *S. americana*. Existió variabilidad entre los sitios en la forma de la curva de decaimiento de la similitud del canto, lo que indica que otros factores además de la distancia también pueden influenciar los patrones de similitud del canto. Encontramos una alta repetibilidad de los cantos individuales en la época reproductiva tanto para machos de segundo año como para los machos de más de dos años, como también una alta conformidad con la vecindad de canto local, tanto para machos de segundo año como para los de más de dos años, desde que se realizó su primera grabación luego de su llegada en mayo. Los machos de más de dos años que retornaron, cantaron el mismo canto que habían producido durante la época reproductiva anterior.

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In many oscine songbirds, songs produced by males in the same area are more similar to each other than to the songs of more distant conspecifics (Lemon 1975, Krebs and Kroodsma 1980, Baker and Cunningham 1985). Such patterns of song sharing have often been termed "dialects," though some researchers limit this designation, for instance, to song sharing at the scale of kilometers or larger (Beecher and Brenowitz 2005) or to cases where all elements of a song differ across a discrete geographic boundary (Mundinger 1982). Conspecific imitation during song development is common in oscine songbirds, so maintenance of predictable geographic differences in songs within a population is contingent on behavioral processes either limiting most individual movement to within the song neighborhood or facilitating the acquisition of local song characteristics after immigration (Krebs and Kroodsma 1980, Cunningham et al. 1987). If males of a species typically disperse from their natal song neighborhood, the young birds may not hear their adult neighbors' songs until their first breeding season and, thus, yearling males may learn a new song to match the local song type (Beecher and Brenowitz 2005).

The precise geographic scale of song sharing is largely unknown in most species. Elucidating these geographic patterns can be an important step in our attempt to understand the interaction between behavioral and ecological processes in shaping song neighborhoods. We know that geographic scales of song sharing vary among (Handley and Nelson 2005), and even within (Bitterbaum and Baptista 1979), species. Some descriptions of geographic patterns of song sharing have been drawn from studies that compare song characteristics between discrete locations (e.g., Marler and Tamura 1964, Tracy and Baker 1999), whereas others have demonstrated song-type turnover among neighboring birds living within a continuously inhabited corridor (e.g., McGregor 1980, Lachlan and Slater 2003, Shieh 2004). For species in which song sharing is limited to a handful of neighbors (e.g., Payne et al. 1988), examining the larger geographic scale of the phenomenon is not necessary. However, in many species, song sharing extends well beyond immediate neighbors, and in most such species the geographic scale of song sharing is unknown. Further, although some hypotheses proposed to explain variation in the geographic patterns of song sharing have been modeled (Williams and Slater 1990, Ellers and Slabbekoorn 2003), they remain almost entirely untested empirically. Lachlan and Slater (2003) found different absolute levels of song sharing among populations of Common Chaffinch (*Fringilla coelebs*), though song sharing tended to peak at ~500 m, which indicates that song tutors in that species are not adjacent neighbors. If, by contrast, males learn their song from adjacent neighbors, resemblance should be high between neighbors and decline as distances between birds increase. However, it is not just the peak, but the entire spatial pattern of song resemblance, that can be informative. For instance, we might expect the spatial scale of song sharing to vary among sites as a result of habitat quality or changes in habitat that lead to differences in bird density or site fidelity (Holland et al. 1996, Laiolo and Tella 2005).

In many species, individuals recognize song elements as belonging to categories and adopt songs to categorically match the songs of neighbors (Horn and Falls 1996, Beecher and Brenowitz 2005), though quantitative variation in song production can also be important (Bell et al. 1998). If song-element categories are relatively stable over time and space, as in Indigo Buntings (*Passerina cyanea*; Shiovitz and Thompson 1970, Payne et al. 1988), describing song sharing in terms of qualitative matching of song elements is likely to be sufficient. However, quantitative differences are often detectable within elements across individuals (e.g., Cunningham et al. 1987, Bell et al. 1998). Imperfect copying of songs may generate this variation, and such cultural "mutation" is probably the ultimate source of different song elements within a species (Lemon 1975, Slater 1986). Thus, quantitative measures of song similarity will complement information about categorical similarity when attempting to understand geographic variation in song.

We studied patterns of song sharing in the Dickcissel (*Spiza americana*), one of the most abundant birds of the eastern Great Plains of North America (Temple 2002). No formal study of its song has been published (Temple 2002), but our casual observations indicated that Dickcissels shared songs with neighbors and that this sharing decreased with distance. In this initial study of song sharing in Dickcissels, we wanted to know (1) whether we could detect variation in song structure within individual males in or between seasons and (2) whether males breeding for the first time showed higher variation in song structure than older males, as might be expected if young males were perfecting their rendition of the local song type. We also sought to (3) document song sharing among neighboring males, (4) determine the spatial scales and patterns of song sharing on the landscape by considering birds ranging in proximity from tens of meters to hundreds of kilometers, (5) look for indications of among-site variation in the scale of song sharing, and (6) assess the extent to which qualitative (element type) and quantitative (note frequency and duration) variation in song contributed to song similarity among males.

Methods

During the breeding season, most male Dickcissels devote a large portion of the day to singing from prominent perches on their territory (Schartz and Zimmerman 1971). When singing, most males produce one song approximately every 3–8 s, and most of these songs last between 1 and 2 s. Most males sing only one song type (see discussion of repeatability below), though slight variations of this song may exist, typically because of occasional omission of an element. We recorded at least three examples of an individual's song during each recording to increase the likelihood of obtaining a sample of high clarity and to avoid missing occasionally omitted elements. For birds that exhibited noticeable variation at the time of recording, we recorded additional songs to get a more complete representation of each bird's song. However, given that within-individual variation normally occurred in number, as opposed to type, of elements, our analyses, which focused on element type and within-element change, were unaffected by most song variability (see below).

We recorded songs of male Dickcissels with a Marantz PMD680 recorder and a Sennheiser short shotgun microphone (ME66). We took Universal Transverse Mercator coordinates at each song recording using a handheld global positioning system.

Unbanded birds.—With the goal of describing both broad-scale geographic variation in song production and within-site song-neighborhood conformity, in 2005 we recorded 371 birds spread among 30 sites in the Flint Hills from northern Kansas to northern Oklahoma (Fig. 1). Sites were all suitable Dickcissel habitat, but management practices varied among locations and

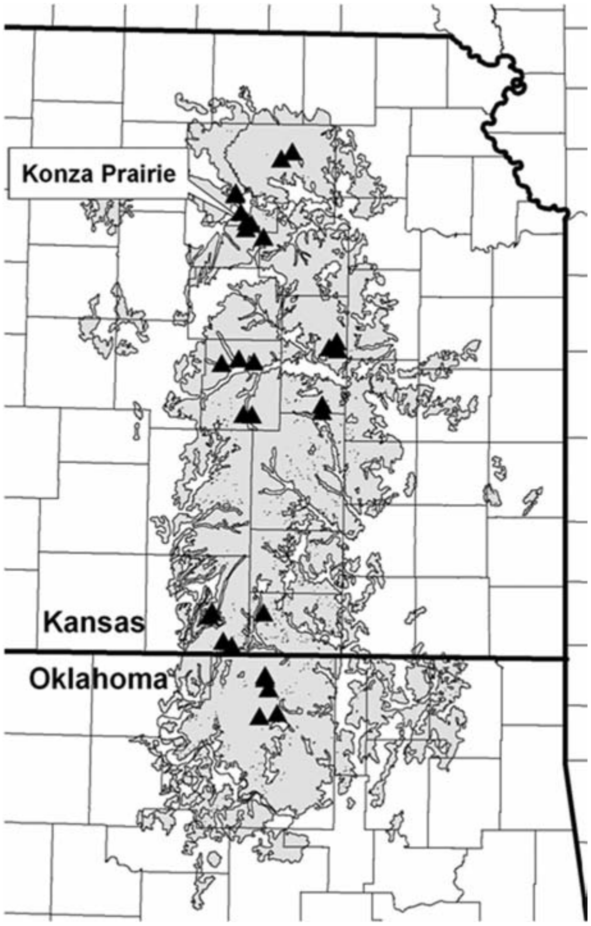

Fig. 1. Triangles represent the 30 sites at which we recorded songs in 2005. Gray is native prairie, primarily in the Flint Hills. Base map courtesy of the Nature Conservancy.

included ungrazed native prairie, prairie grazed by cattle, mowed hay meadows, and Conservation Reserve Program fields (former agricultural fields planted with native grasses). Sites were all in a grassland landscape matrix.

To investigate small- and intermediate-scale sharing, in 2006 we recorded 565 birds in a ~10-km^2 portion of the Konza Prairie Biological Station (KPBS; Fig. 2), a 3,487-ha tract of tallgrass prairie in northern Kansas (39°05′N, 96°35′W). Our goal was to record a large number of birds on contiguous or nearly contiguous territories within an extensive tract of suitable habitat.

To investigate song changes over an intermediate spatial scale, we sampled three road transects (RT) located within 60 km of KPBS (RT1: 12 km, $n = 40$ birds; RT2: 19 km, $n = 33$ birds; RT3: 22 km, $n = 33$ birds; Fig. 2). One observer slowly drove infrequently traveled country roads and stopped to record a Dickcissel whenever one was heard within ~100 m of the road. Habitat along road transects included grazing land, row-crop agriculture, and small amounts of riparian forest and hedgerows. Presumably because of this heterogeneity, Dickcissel distribution was often clumped.

We recorded all songs between dawn and 1200 hours CST. If we located a male that did not produce a recordable song in ~1 min, we moved on and omitted it from the study. When working with unbanded birds, there is a risk of recording the same individual more than once. Fortunately, Dickcissels sing frequently, and it is relatively easy to locate and keep track of multiple individuals simultaneously in the open prairie. By paying careful attention to the Dickcissels in the vicinity, and by not moving back through areas in which we had previously recorded, we are confident that we minimized the risk of making duplicate recordings. There was almost no chance of recording the same bird twice on road transects.

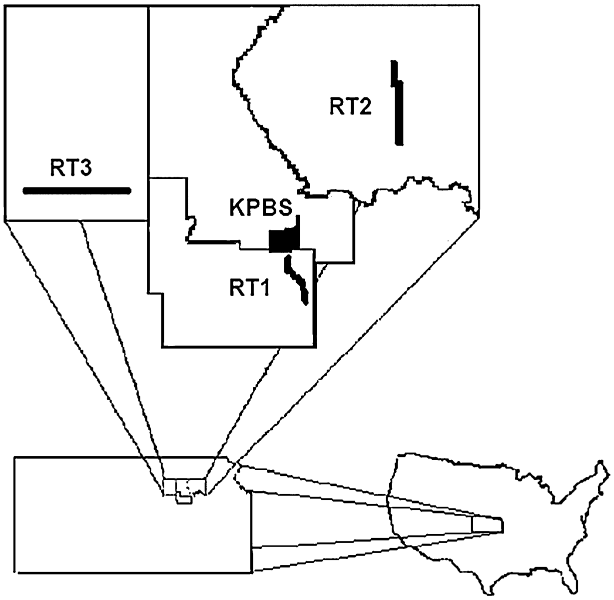

Fig. 2. The four study sites in 2006 located in northeastern Kansas: Konza Prairie Biological Station (KPBS), primarily in Riley County; road transect 1 (RT1), 12 km in Geary County; RT2, 19 km in Pottawatomie County; and RT3, 22 km in Clay County.

Banded birds.—In 2006, our research group and another independent researcher (Bridget Sousa) mist netted male Dickcissels and banded them with U.S. Fish and Wildlife Service and color bands at KPBS. To lure the targeted bird, song of another Dickcissel was played near the mist net(s). We used tail-feather morphology to determine whether the 21 birds our research group banded were second-year (SY) or after-second-year (ASY) (Pyle et al. 1997), though Sousa did not assess age. We assessed age to determine whether the two age classes differed in song change over the breeding season. We recorded each bird of known age for the first time immediately after banding between 19 and 31 May. We returned multiple times through the summer (1 June–11 July) to locate and re-record the banded males. At each successive recording, we confirmed bird identity by inspection of color bands. If a banded bird had been replaced by an unbanded bird in any given week, we assumed that it had been permanently displaced and discontinued pursuit of the missing bird. Of the 34 banded birds, 2 were recorded only once (these were excluded from analysis), 6 (4 of known age) were recorded twice, 2 (both of known age) were recorded three times, and 24 (13 of known age) were recorded four times. Whether the individuals recorded were of known age or not, repeated recordings allowed us to assess the consistency of song structure throughout the season and the suitability of our method of using brief recordings of unbanded birds to describe their song.

We attempted to relocate returning banded males at KPBS in May 2007. We found and recorded songs of 8 of the original 34 banded birds, all on or near the sites of their 2006 territories. This allowed us to determine whether males returning to the same breeding site alter their song structure between years.

ANALYSES AND RESULTS

Qualitative description.—We could readily distinguish songs from different locations by ear, but some of the more subtle within-site variation was detectable only by examining sound spectrograms. We visually assessed sound spectrograms from all recordings using RAVEN, version 1.2 (Cornell Lab of Ornithology 2005). We separated each song into multiple phrases. Complex phrases were further subdivided into multiple elements, but simple phrases were considered to consist of a single element (Fig. 3). We identified distinct elements by the presence of unique combinations of notes consistently found together (Fig. 3). All Dickcissel songs comprised two or three phrase classes. First came one to several phrases belonging to the *dick* class (range: 0–12, mode = 2, mean = 2.7). Because *dick* phrases were short and simple, each *dick* phrase consisted of a single element. This series of *dick* phrases was followed by one to several longer *cissel* phrases (range: 0–5, mode = 3, mean = 2.6). Because of the longer duration, higher variation, and partially independent turnover of groups of notes within each *cissel* phrase, we divided each phrase into an introductory, intermediate, and terminal element (Fig. 3). We occasionally encountered a third phrase type, a trill located between the *dick* phrases and *cissel* phrases or following the *cissel* phrases. A trill contained the same element repeated multiple times and, thus, was classified as a single element type. The songs of 186 of 1,043 individuals contained trills. Although trills could be located before or after the *cissel* phrases, the same trill structures were sometimes found in one position in the song in one bird and in the other position in another. Thus, we did not distinguish between trills on the basis of their location in the song, but only on the basis of noticeable differences in structure. Although the trill phrase was often absent, songs rarely lacked *dick* or *cissel* phrases. The only phrases that were subdivided into more than one element were *cissel* phrases, but we use the term "element" throughout the present study to refer to the smallest unit of classification of Dickcissel song components to facilitate simple descriptions of our analyses and results. In cases where a bird sang multiple *dick* phrases in the same song, these phrases were not always of the same element type (115 of 1,043 birds sang >1 *dick* element type; maximum number of types = 4). Some birds produced two different sets of *cissel* phrases in the same song (54 of 1,043 birds), a series of one set of elements followed by a series of another composed wholly or partly of different elements. Individual songs were composed of three to seven unique elements (including all those from the *dick*, *cissel*, and trill phrases); most contained either four or five. For each of the element classes, we created an element library. In every song, we assigned each element a number representing an element

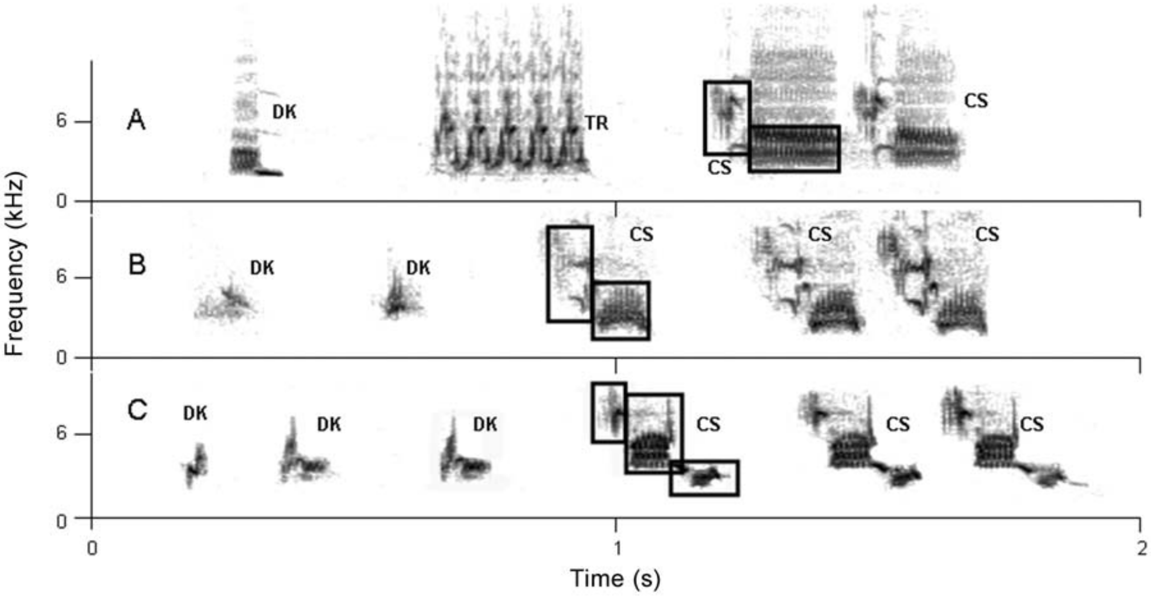

FIG. 3. Three Dickcissel songs from three distinct vocal neighborhoods. In these examples, *dick* (DK) phrases differed in number among males, one song contained a trill (TR), and *cissel* (CS) phrases were sung either two or three times. We divided our *cissel* phrases into two (A, B) or three (C) elements (in boxes). The first *cissel* element was typically a set of relatively high-frequency notes, the second element most often contained a buzzy series of notes of high bandwidth, and the third element was most typically a low-frequency "tail." We did not subdivide *dick* or trill phrases for classification. We identified an "element type" as a readily discernible, unique combination of notes. Therefore, the *dick* element type in song A is readily classified as distinct from any of the other *dick* elements, and each of these three songs can be seen to contain a different set of *cissel* elements. See text for further explanation.

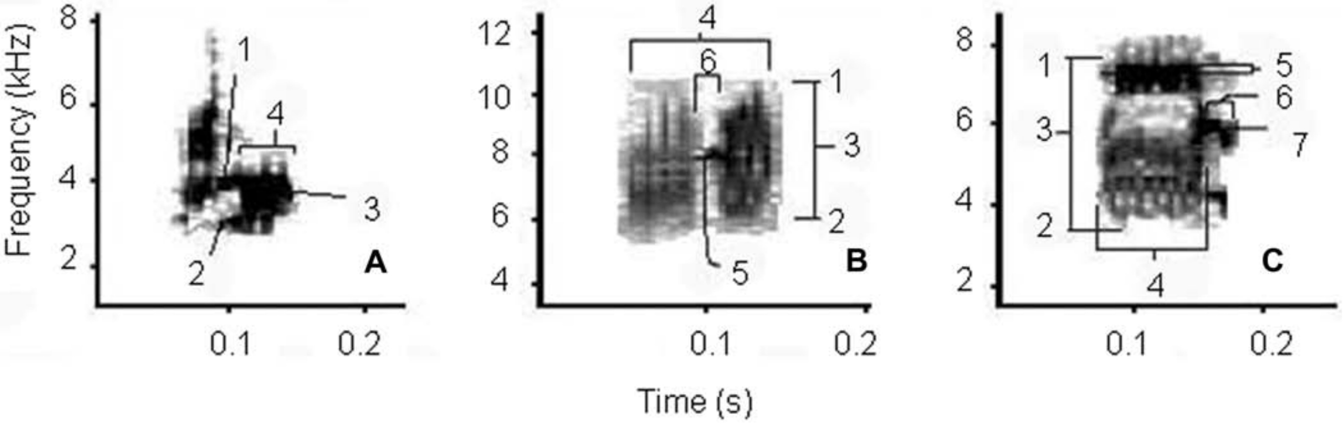

FIG. 4. (A) The four measures used to quantify element type DK#1 (DK = *dick*). 1, 2, and 3 are frequency (kHz) measures taken at an early high, early low, and terminal point, respectively, and 4 is the duration (s) of the element's "tail." (B) The six measures used to quantify element type CS1#1 (CS = *cissel*). 1 and 2 are the high and low frequencies of the element, respectively, 3 is the element's frequency range, 4 is the element's duration, 5 is the average frequency of the dash, and 6 is the slope (ΔkHz/Δs) of the dash. (C) The seven measures used to quantify element type CS2#1. 1 and 2 are the high and low frequencies of the element, respectively, 3 is the element's frequency range, 4 is the duration (s) of the element's main part, 5 is the slope of the element's top, 6 is the slope of the tail, and 7 is the tail's average frequency.

type from the library or, if we encountered an element type that did not fit into any existing category, we added a new entry to the library. P.J.W. classified the 2005 recordings, and D.M.S. classified the 2006 recordings. Because of the different geographic locations of these recordings, we used independent libraries. Final library sizes were as follows: 2005, *dick* = 56, *cissel* 1 = 39, *cissel* 2 = 42, *cissel* 3 = 27, trill = 27; and 2006, *dick* = 44, *cissel* 1 = 39, *cissel* 2 = 41, *cissel* 3 = 21.

To determine whether elements are recognized as distinct by the birds requires playback experiments (Horn and Falls 1996), and we did not conduct such experiments. However, when playback experiments are conducted, birds of other species appear to classify song elements and often do so in a manner similar to the classification schemes of the humans studying them (Horn and Falls 1996). Further, qualitative comparison of song elements is the most common method used to describe song sharing (e.g., Miyasato and Baker 1999, Tracy and Baker 1999, Nelson 2000, Shieh 2004). However, even if classifications are recognized by the birds themselves, by limiting analyses to song categories, researchers overlook quantitative variation, which may be an important component of geographic variation in song sharing.

Quantitative description.—Grouping song elements into types facilitated quantitative measurements within element types that shared the same notes and structure. We measured duration and frequency of notes (or groups of notes) to quantitatively analyze among-individual variation within an element. We took such measurements for all birds recorded at KPBS in 2006 singing any one of three common element types that we designated "*dick* element, type one" (DK#1, $n = 550$ birds; Fig. 4A), *cissel* element one type one (CS1#1, $n = 79$; Fig. 4B), and "*cissel* element two, type one" (CS2#1, $n = 55$; Fig. 4C). We also quantitatively measured portions of the *dick* and *cissel* phrases for each of the 32 banded birds recorded multiple times (Fig. 5).

Repeatability.—Multiple recordings of banded birds revealed that Dickcissel songs remained mostly constant throughout the breeding season among birds maintaining a single territory. In the 32 banded birds recorded on multiple days in 2006, 133 of 145 (91.7%) elements detected were recorded in the first recording. We did not detect additional song elements in subsequent recordings for 25 of 32 individuals. It is likely that across our four brief recording sessions we did not detect all the song elements in the repertoires of all 32 birds. However, the rarity of detecting additional song elements in different recording sessions suggests that we detected most elements and demonstrates that most birds sang a single set of elements most of the time. Repeatability analyses (Lessells and Boag 1987) for each of six quantitative song measures (Fig. 5) revealed highly significant results ($r = 0.70$–0.96, $P < 0.001$ for all measures). Therefore, separate recordings of an individual's

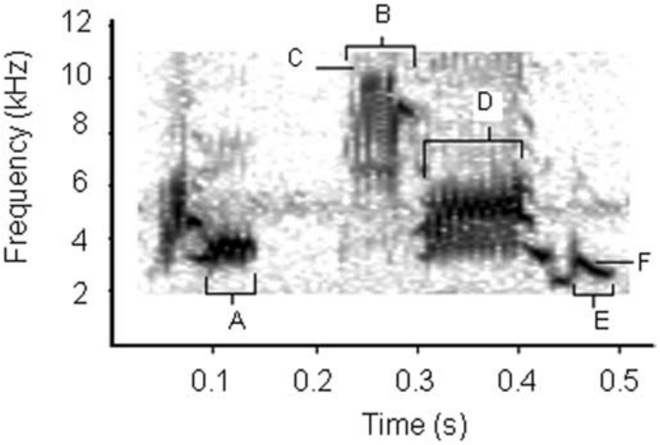

FIG. 5. The six measurements tested in repeatability analysis of banded birds. Measurements represent (A) DK (= *dick*) element "tail" duration (s), (B) CS1 duration (CS = *cissel*), (C) song high frequency (kHz), (D) CS2 duration, (E) duration of the tail of CS3, and (F) CS3 tail average frequency.

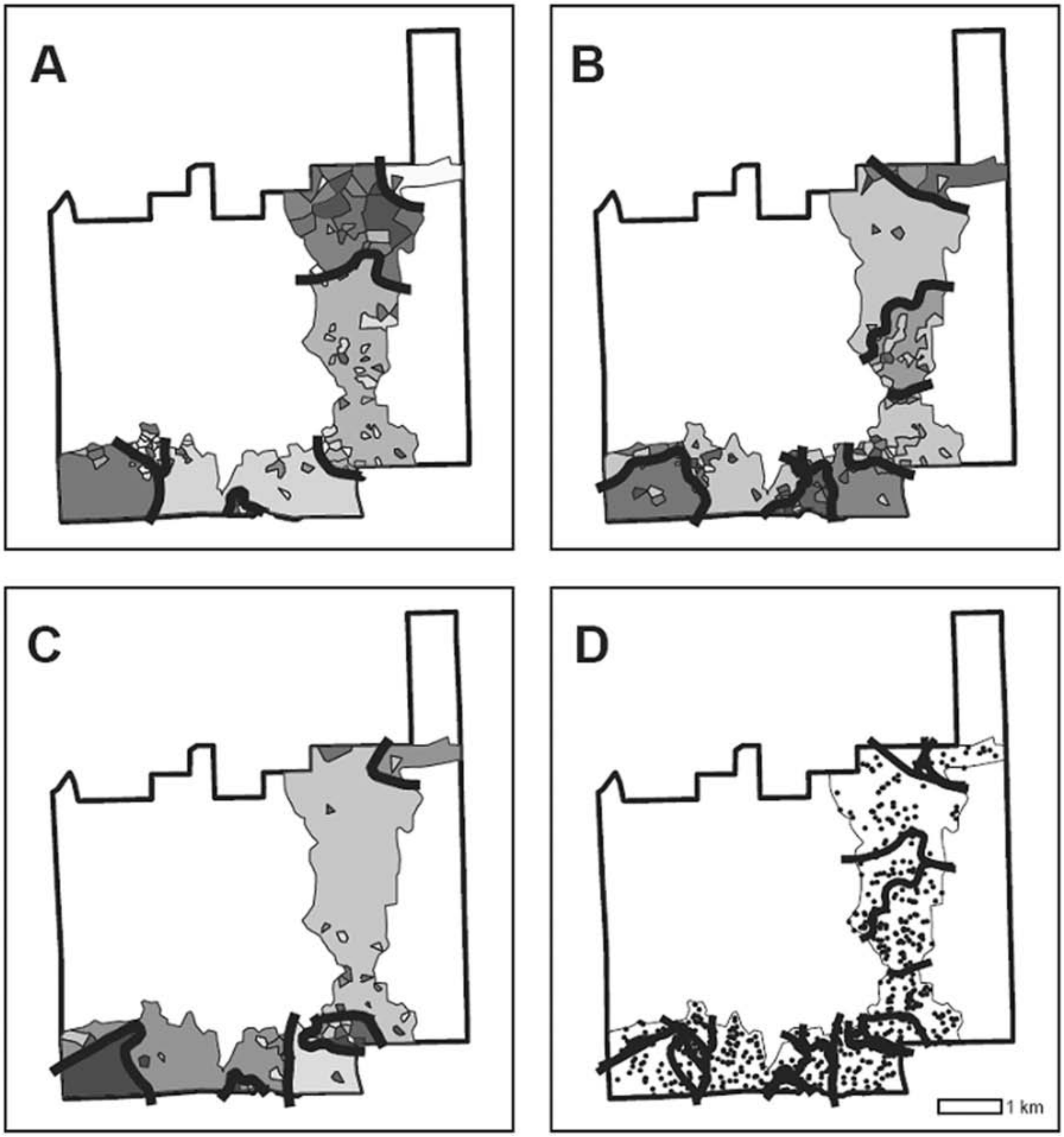

FIG. 6. Distribution of element types recorded at Konza Prairie Biological Station (KPBS) in 2006 for (A) *cissel* element 1, (B) *cissel* element 2, and (C) *cissel* element 3. Thick black lines indicate approximate geographic boundaries between element types. The fourth map (D) shows the partial congruence of dividing lines between element types for all three *cissel* elements. Map D also depicts the locations of all recorded birds.

song are highly consistent. This result justifies our use of single recordings to describe an individual's song, our comparisons of songs recorded on different dates, and our use of quantitative measures of note characteristics. Banded males returning in 2007 did not appear to change their song structure between years. Each male's song elements belonged to the same categories in both years.

Age effects.—We found no evidence of age effects on song in Dickcissels. Because we identified very little change in songs of males throughout the breeding season (see above), no difference was detected between SY and ASY birds in terms of changes in qualitative song-element classification. We also compared the coefficient of variation (CV) for measured song traits between SY and ASY individuals. For this analysis, we summed the CVs across song traits for each banded bird of known age class and compared these sums between SY and ASY birds using Student's t test, but there was no difference (SY: mean = 0.061 ± 0.007 [SE]; ASY: mean = 0.078 ± 0.016; $t_{30} = 0.79$, $P = 0.44$).

Spatial turnover of element types.—To determine whether song neighborhoods had sharp boundaries, we examined maps of the distributions of element types for the KPBS 2006 data (Fig. 6). First we produced three maps, one each for the first, second, and third element of the *cissel* phrase. We used ARC-GIS

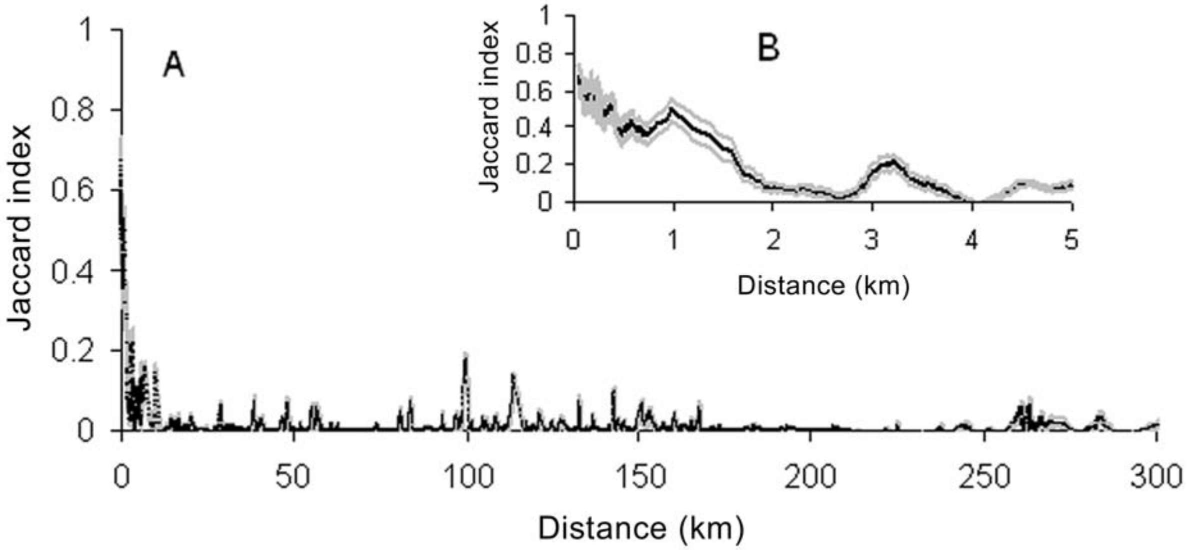

Fig. 7. (A) Distance (km) plotted against the Jaccard index of pairwise song similarity, based on entire song (elements from all phrases analyzed together), for all pairwise comparisons of birds recorded across the Flint Hills region in 2005. (B) The decline in song sharing over small to intermediate distances is more clearly evident when a subset of the plot is examined, limited to those pairs within 5 km of each other. Higher values along the *y* axis indicate a larger portion of shared song elements. Black lines = means, and gray lines = 95% confidence interval.

(ESRI, Redlands, California) to place Thiessen polygons around the coordinates for each individual, and we colored each polygon according to the song-element classification of that bird. Thiessen polygons encompass the area falling closer to a given point than to any other points. We selected this method because it produced maps that were much easier to read than ones in which element-type locations were coded by colored dots or symbols. We then drew lines dividing areas dominated by different element types. On a fourth map, we superimposed these dividing lines to allow us to observe whether elements in different positions in the Dickcissel song had concordant geographic distributions and boundaries (Mundinger 1982).

Our maps indicated that a change in element type in one portion of the *cissel* phrase often occurred in similar geographic locations as a change in element type in another portion of the *cissel* phrase (Fig. 6). However, boundaries between element types for different portions of the *cissel* phrase were not perfectly correlated with each other, which indicates that songs are not necessarily always learned in their entirety from a single tutor. For any given element type, especially the common ones, individuals singing that element type were mostly clustered together. However, for all three *cissel* elements, some individuals sang element types that did not match their neighbors, and some small areas seemed to be dominated by more than one element type (e.g., northern; Fig. 6A). Thus, not all individuals match the song elements of their neighbors.

Song similarity versus distance based on element classification.—We analyzed song similarity in the 2005 data, the 2006 KPBS data, and each of the three 2006 road-transect data sets separately. We examined song similarity between all possible pairs of individuals within each of the five data sets using the Jaccard index (JI; Podos et al. 1992, Tracy and Baker 1999, Lachlan and Slater 2003).

For birds recorded in 2005, we calculated each data point as the mean song similarity of 100 pairs of birds. The first point was the average JI for the closest 100 bird pairs, the JI for the second point was the average for pairs 11–110, and so on. By including individual paired comparisons in multiple data points, we created a rolling average and, thus, a smoother curve (see Lachlan and Slater 2003) on our plot of average JI versus average distance between pairs of birds (Fig. 7). We used bootstrapping (Efron and Tibshirani 1993) to calculate confidence intervals (CIs) for song sharing as measured by JI. For each group of 100 bird pairs point^{-1}, we subsampled an equal number of pairs with replacement and calculated mean song sharing for that subsample. We repeated this procedure 1,000 times to generate a distribution of JI values. We calculated 95% CIs using the percentile method (2.5th and 97.5th percentiles). We coded all simulations in Microsoft VISUAL C++, version 6.0 (Microsoft, Redmond, Washington).

In the recordings from 2005, Dickcissels showed high song similarity within sites but no obvious relationship between among-site distance and among-site song similarity for the 30 sites spread throughout the Flint Hills (Fig. 7). Although we found occasional spikes of song similarity at certain distances between birds at different sites, these spikes were low compared with the high peak at very short (within-site) distances, and the among-site spikes in song similarity were found between both close and far sites (Fig. 7). Of the nine sites from 2005 with the largest samples of recorded birds (*n* range: 16–29, mean = 19.6), three showed significant decline in song similarity with increasing pairwise distance on the site, and six showed no significant change in song similarity (data not shown). Pairwise distances at these sites were almost all very small (<500 m).

Details of the analysis of 2006 KPBS birds differed slightly from the analysis of 2005 data. For KPBS data, we calculated each initial data point as the mean song similarity of 40 pairs (i.e., JI for the first point is the average JI for the closest 40 bird pairs, JI for the second point is the average for pairs 41–80, etc.). To display a

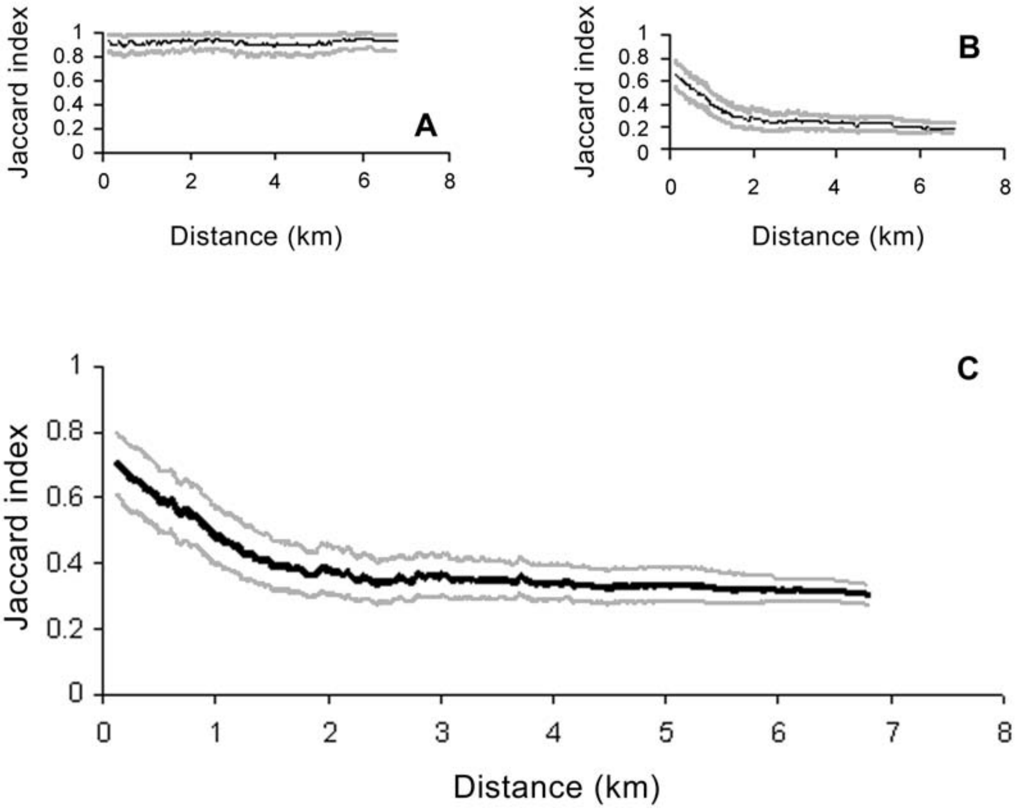

FIG. 8. Distance (km) plotted against the Jaccard index of pairwise song similarity for all pairwise comparisons of birds recorded at Konza Prairie Biological Station (KPBS) in 2006 for (A) *dick* elements only, (B) elements from the *cissel* phrase, and (C) entire song (*dick* and *cissel* elements analyzed together). Higher values along the *y* axis indicate a larger portion of shared song elements. Black lines = means, and gray lines = 95% confidence interval.

smoothed function of how song sharing varies with distance between individuals, we constructed a figure with a rolling average of 50 initial points (for a total of 2,000 pairs point^{-1} = 40 pairs initial point^{-1} × 50 initial points; e.g., Lachlan and Slater 2003). Our bootstrapping procedure to generate CIs was identical to that described above, except that we sampled within our groups of 40 pairs rather than groups of 100 pairs.

This analysis revealed strong song sharing at short distances between Dickcissels and decreasing sharing with increasing distances between pairs of birds at KPBS (Fig. 8). However, the decline was not linear and, on average, bird songs 7 km distant were no less similar than those 2 km distant, at least in the continuous habitat of KPBS (Fig. 8). This trend was largely driven by the *cissel* elements (Fig. 8B). Because nearly all birds on the site sang the same *dick* element, no decline in the sharing of this element could be detected with distance (Fig. 8A). Ninety-five percent CIs indicate that overall song sharing was significantly higher between the nearest 2,000 pairs of birds (mean = 130 m between birds; JI = 0.704) than for birds located ≥1 km apart (JI = 0.478; Fig. 8C). Similarly, examination of 95% CIs illustrates that pairs of birds located within 0.8 km (JI = 0.544) of each other demonstrated significantly more song sharing than birds located ≥2 km apart (JI = 0.376; Fig. 8C).

We conducted our analyses of qualitative song similarity among birds on the 2006 road transects in a manner identical to that of the 2005 data. On road transects, birds near each other showed moderate song sharing, and sharing was lower between birds more distant from each other (Fig. 9). Road transect 1 (RT1), where Dickcissel density was the highest and habitat appeared to be least fragmented (D. M. Schook and W. E. Jensen pers. obs.), had the highest sharing (JI = 0.53–0.32). On RT2, we found a logarithmic decline in song sharing as distance between birds increased (JI = 0.40–0.01), with essentially no sharing between birds located ≥6 km apart. Similarly, on RT3, we observed a strong logarithmic decline (JI = 0.48–0.07), with the decline leveling off at ~8 km between birds. On all three road transects, values of song sharing decreased significantly ($P < 0.05$ based on examination of CIs) as distance between pairs of birds increased. Bird pairs <2 km apart were more similar than bird pairs >4.5 km apart and, likewise, pairs <4.5 km apart were more similar than pairs >6.5 km apart. The three road transects differed from each other and from the other data sets in the shape of the decay in song similarity with distance.

Song similarity versus distance based on element measurements.—We compared geographic distance to quantitative estimates of song dissimilarity separately for each of our three measured song elements. For each of the three elements, we took multiple measurements that differed in variability, and we accounted for the presence of multiple measurements in two ways. First, to avoid weighting differences in one measurement more or

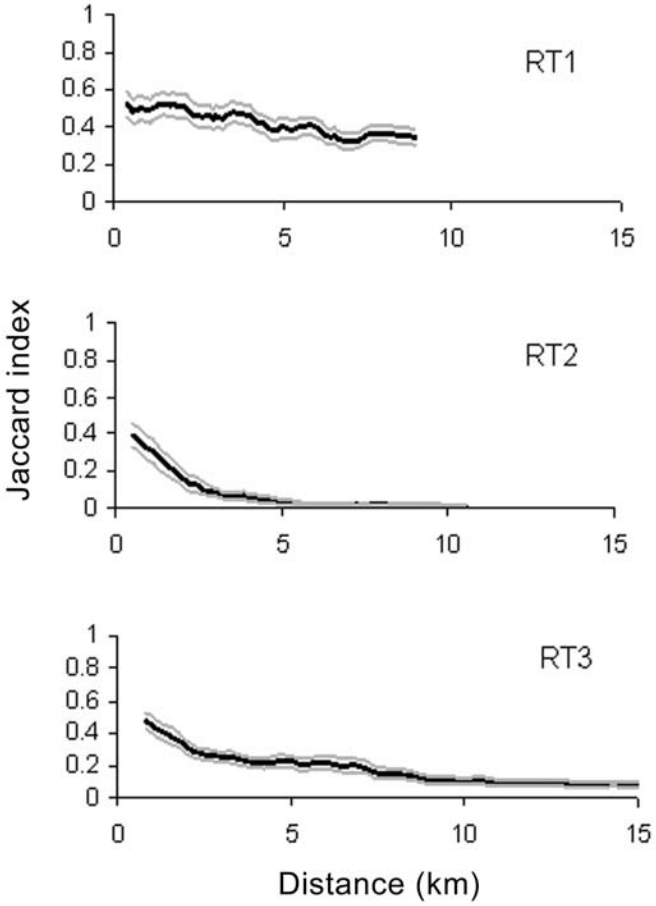

Fig. 9. Distance (km) plotted against the Jaccard index of pairwise song similarity, based on entire song (*dick* and *cissel* analyzed together), for all pairwise comparisons of birds recorded on the three road transects in 2006. Higher values along the *y* axis indicate a larger portion of shared song elements. Black lines = means, and gray lines = 95% confidence interval.

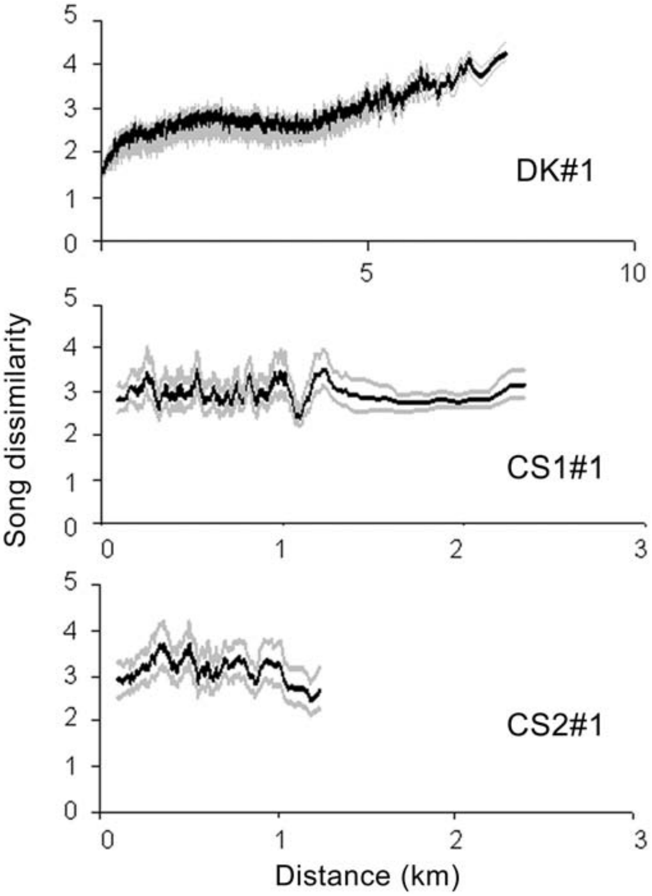

Fig. 10. Patterns of quantitative within-element type difference for three element types: DK#1, CS1#1, and CS2#1 (DK = *dick* and CS = *cissel*). Higher *y*-axis values represent greater differences in elements between pairs of birds. Black lines = means, and gray lines = 95% confidence interval. Note that the *x*-axis scale differs among graphs.

less than differences in other measurements on the basis of scale of variability, we standardized all measurements in units of standard deviations. Second, we compared all pairs of males on the basis of each standardized measurement separately and, then, on the basis of these multiple differences, estimated the total Euclidean distance (hypotenuse in multidimensional space) between pairs of males. This produced an overall estimate of song dissimilarity. We then used the same procedure described above for qualitative song-element comparisons, first calculating a mean dissimilarity among points of similar geographic distance in batches of 100, and moving up in increments of 10 to construct a rolling average to smooth the line. We then used a bootstrapping procedure as described above to generate 95% CIs around these means.

Using the KPBS 2006 data, we observed a clear positive relationship between element dissimilarity and distance for the most common *dick* element, DK#1 (Fig. 10). Bird pairs located within 300 m had a DK#1 element dissimilarity value of <2.05, which, examination of 95% confidence intervals indicates, was significantly lower than that of pairs located >750 m apart, which had an element dissimilarity value of >2.32. Likewise, pairs located within 750 m were significantly more similar than pairs located >4,000 m apart. We also compared pairwise distance to quantitative measurements of two *cissel* elements. For these two elements, which were sung by far fewer birds spread over a smaller area than the *dick* element described above, we observed no relationships between pairwise distance and quantitative measures (Fig. 10).

Discussion

This initial examination of song in Dickcissels produced several principal results. We demonstrated that individual SY and ASY males sing the same song elements with a high degree of consistency both within and between years. Further, high degrees of song similarity existed within sites with predictable declines in song similarity over intermediate distances up to ~10 km. However, at greater distances, song sharing was typically low or absent and variation in song sharing was unrelated to distance between males. We found that although common song elements were typically shared by approximately discretely bounded groups of individuals, different song elements were not always replaced at the same boundaries. Additionally, song elements sometimes differed in the spatial scale of their distribution, as with *dick* and *cissel* elements at KPBS. Similarity among neighboring males was attributable primarily to sharing of song elements, but for one song element shared by many males, quantitative similarity of that element between pairs of males was a function of distance and was highest among neighbors. The shape of the decay of song similarity with distance varied among sites and between elements of the two primary phrase types (*dick* and *cissel*) of the Dickcissel song.

Our observation of consistent song-element production by individuals throughout the season and between years has several implications. At a mundane level, it justifies our use of single brief recordings as sufficient to explain a male's song structure and indicates that our quantitative measurements of songs were sufficiently precise. More interesting, it suggests that, at least for adults that return to the same territories between years, song structure, once determined, does not change. However, we have not conclusively demonstrated that Dickcissels are closed-ended song learners (Beecher and Brenowitz 2005), because we do not know whether a male's song changes when he abandons a territory and attempts to breed elsewhere, apparently a frequent occurrence in this species (Zimmerman 1993). However, we encountered occasional males whose songs did not conform to their local song neighborhood, which suggests that males that move among song neighborhoods may not learn the new song types and that Dickcissels may, in fact, be closed-ended song learners.

It seems likely that males must learn their local song type upon arrival on the breeding grounds after their first winter. We have come to this tentative conclusion because song similarity among individuals declines steadily over relatively short distances and because no banded nestlings have ever been found as adults (Temple 2002), which suggests very little local recruitment. In some species with this pattern, yearling males may adopt the songs of neighbors well after settling on and defending a breeding territory (e.g., Payne et al. 1988). However, our observation that yearling males produced the local song type perfectly at first recording in May, and had no greater variation in song-element production than older males over the course of the season, suggests that if males are learning or perfecting their song after their first winter, this task is accomplished almost immediately after arrival on the breeding ground. In Dickcissels, yearlings begin to occupy breeding territories several days or even weeks after territorial older males (W. E. Jensen and T. H. Parker pers. obs.), and some of this delay may involve yearlings learning the local song type before claiming a territory. This may explain our failure to observe a learning period, given that we were able to capture, band, and monitor only males that were already singing and territorial.

Song sharing was most striking among adjacent or nearly adjacent males and tended to decline logarithmically to a maximum distance of ~10 km. This is consistent with the idea that neighbors are song tutors in Dickcissels, a common pattern in many species (Krebs and Kroodsma 1980), but in contrast to a recently reported pattern of peak song sharing at 500 m in Common Chaffinches (Lachlan and Slater 2003). We noticed partially correlated spatial turnover in some elements at small or intermediate scales. Although we have no evidence that *dick* and *cissel* elements change together, different elements in the *cissel* phrase seemed to have geographic ranges somewhat related to each other. Because only some elements appear to be spatially correlated at the scales we examined, the Dickcissel seems to more closely resemble species that show different turnover location for some different elements (e.g., Bitterbaum and Baptista 1979), rather than those showing sharp boundaries at which effectively all song elements turn over (e.g., Bjerke and Bjerke 1981). The pattern we observed of song sharing declining over small to moderate scales is consistent with song learning from neighbors as the mechanism promoting geographic conformity in song production (Krebs and Kroodsma 1980).

Several explanations have been proposed to explain song sharing by neighbors. Postdispersal song learning from neighbors can lead to geographic patterns of song sharing regardless of adaptive function (Slater 1986), though this still leaves the question of why birds should learn songs from adult neighbors, especially given that not all songbirds do so (Kroodsma 1996). In species with song repertoires of >1, individual birds can signal different information by singing different songs from their repertoires. For instance, during countersinging with a neighbor, matching that neighbor's current song type ("song-type matching") may occur in different social contexts than choosing a different song from that neighbor's repertoire ("repertoire matching") (Beecher et al. 2000). In species like the Dickcissel, where each individual's repertoire typically contains only one song type, individuals cannot adjust their song types to respond to different neighbors or contexts. However, there may still be benefits to sharing songs with neighbors—for instance, if individuals with local song elements are recognized and, therefore, face fewer aggressive challenges (Payne 1983, Lachlan et al. 2004). Further research is required to test the applicability of such hypotheses to Dickcissels.

On KPBS, a striking example of variation in the geographic scale of song sharing merits discussion. One *dick* element was sung by most individuals on this site, whereas we observed many combinations of *cissel* elements and no single set of *cissel* elements dominated the site. This could indicate the sort of pattern described in White-crowned Sparrows (*Zonotrichia leucophrys*), in which certain aspects of the song vary predictably at broader geographic scales (often termed "dialects" in studies of that species) and other measures of song vary at a smaller scale (Cunningham et al. 1987). To further test the applicability of this White-crowned Sparrow model to Dickcissels, we need to consider broad-scale spatial sampling to identify patterns of turnover of widespread elements. Our initial examinations at potentially relevant scales on our three road transects did not support this model. Qualitative sharing of the *dick* element was similar to sharing of *cissel* elements (data not shown). Thus, the pattern at KPBS may be a special case rather than a general difference in geographic scale of song sharing between these phrase types.

Some authors reserve the term "dialect" for cases in which song types are divided by discrete geographic boundaries (Mundinger 1982). This definition appears to exclude Dickcissels, given that only some components of their song change at the same spatial boundaries. There are species in which dialect boundaries appear to be unambiguous by any measure (e.g., Redwing [*Turdus iliacus*]; Bjerke and Bjerke 1981). However, in others, including the classic dialect case of the White-crowned Sparrow, certain notes or elements are shared across dialects (Baptista 1975), there is both qualitative (Baptista 1975) and quantitative (Bell et al. 1998) variation within putative dialect areas, and dialect boundaries are not completely discrete (Baptista 1975). In Dickcissels, definition of the boundary of a discrete dialect area would depend on which components of the song we chose to designate as diagnostic of the dialect and the degree to which we split or lumped song-element categories. However, high local conformity across song elements, ready detection by human ear of song similarity at moderate spatial scales (multi-kilometer), and relatively discrete boundaries between element types suggest that shared songs in Dickcissels could be referred to as "dialects."

Both element turnover and quantitative within-element changes contribute to formation of distinct vocal neighborhoods. Variation in song is often described in terms of element categories, and these descriptions have proved useful (e.g., Marler and Tamura 1964, Tracy and Baker 1999); however, exploring within-element variation may produce different insights. The presence of quantitative variation supports the hypothesis that copying errors lead to changes in song elements and, presumably, ultimately to the creation of new elements (Lemon 1975, Slater 1986). We should point out, however, that only one of our three quantitatively measured elements showed a relationship between sharing and distance. This element type was sung by hundreds of birds recorded across much of KPBS. By contrast, the other two elements in which quantitative variation was unrelated to distance were each sung by <100 individuals spread over much smaller portions of KPBS. Thus, it seems that the generation of predictable quantitative spatial variation in song-element production may require an element type sung by many birds and spread over an adequately large range. If changes over time depend on the same copying-error mechanism we hypothesize for changes over distance, this result suggests that relatively long periods may be needed for within-element evolution to occur in a locality in this species.

Although we observed declining song similarity with distance in multiple locations, the shape of the relationship varied. We hypothesize that two main factors influence the spatial scales of song sharing: male density and among-year turnover of males. Different habitats support different densities of Dickcissels (Zimmerman 1971, Powell 2006) and within-year observations of territory abandonment suggest that male turnover differs among habitats as well (Zimmerman 1993). Our data on song similarity at intermediate distances came from four locations that differed from each other in habitat in multiple ways. The two sites with moderate song sharing beyond 5 km (KPBS and road transect 1) were both composed primarily of continuous grassland, whereas the two sites with low-to-absent song sharing at 5–10 km (road transects 2 and 3) were in more heterogeneous landscapes. This suggests that observed variation in the scale of Dickcissel song neighborhoods may be influenced by habitat. The relevance of density and turnover to song-sharing dynamics has received little consideration. Some evidence supports a role for one or the other of these mechanisms in a few other song-sharing systems (Holland et al. 1996, Lachlan and Slater 2003, Laiolo and Tella 2005), but only an effect of density has been explicitly tested (Laiolo and Tella 2005), and this only at the scale of adjacent or nearly adjacent territories. Tests of the role of these mechanisms in shaping the geographic patterns of vocal sharing are needed.

Our results demonstrate that explicit consideration of spatial distributions of culturally influenced behaviors can lead to the generation of hypotheses concerning behavioral ecological processes. Few studies of bird song or other avian behaviors have attempted to thoroughly describe their spatial variation at multiple scales, but this will be an important component of continued progress in these fields.

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