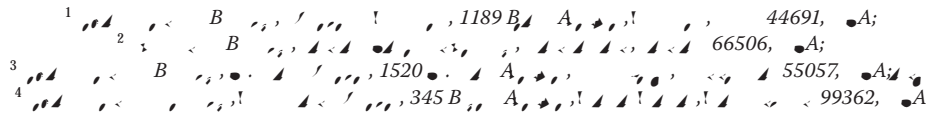







## GEOGRAPHIC PATTERNS OF SONG SIMILARITY IN THE DICKCISSEL

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



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**A** .—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  $\dots$  individuals, we investigated song sharing in Dickcissels (, ) 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  $\sim$  km. At the largest spatial scales ( $\dots$  km between sites), there was very little similarity among sites and no obvious tendency for a decrease in similarity with increasing distances among our  $\dots$  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.  $\dots$  us, 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. 

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

Pa e Ge g a c e a S d de Ca e *Spiza americana*

**R** .—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  $\dots$  individuos, investigamos la similitud del canto en ,  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  $\sim$  km. A la escala espacial mayor ( $\dots$  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  $\dots$  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 influyó tanto la similitud cuantitativa como la similitud cualitativa del canto en , . 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 songbirds, songs produced by males in the same area are more similar to each other than to the songs of more distant conspecifics (Lemon , Krebs and Kroodsma , Baker and Cunningham ). 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 ) or to cases where all elements of a song differ across a discrete geographic boundary (Mundinger ). 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 , Cunningham et al. ). 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 ).

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 ), and even within (Bitterbaum and Baptista ), 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 , Tracy and Baker ), whereas others have demonstrated song-type turnover among neighboring birds living within a continuously inhabited corridor (e.g., McGregor , Lachlan and Slater , Shieh ). For species in which song sharing is limited to a handful of neighbors (e.g., Payne et al. ), 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

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 we recorded birds in a ~ -km portion of the Konza Prairie Biological Station (KPBS; Fig. ), a , -ha tract of tallgrass prairie in northern Kansas (

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 . We found and recorded songs of of the original banded birds, all on or near the sites of their territories.

is allowed us to determine whether males returning to the same breeding site alter their song structure between years.

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#### ANALYSES AND RESULTS

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—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 . (Cornell Lab of Ornithology ). We separated each song into multiple phrases. Complex phrases were further subdivided into multiple elements, but simple phrases



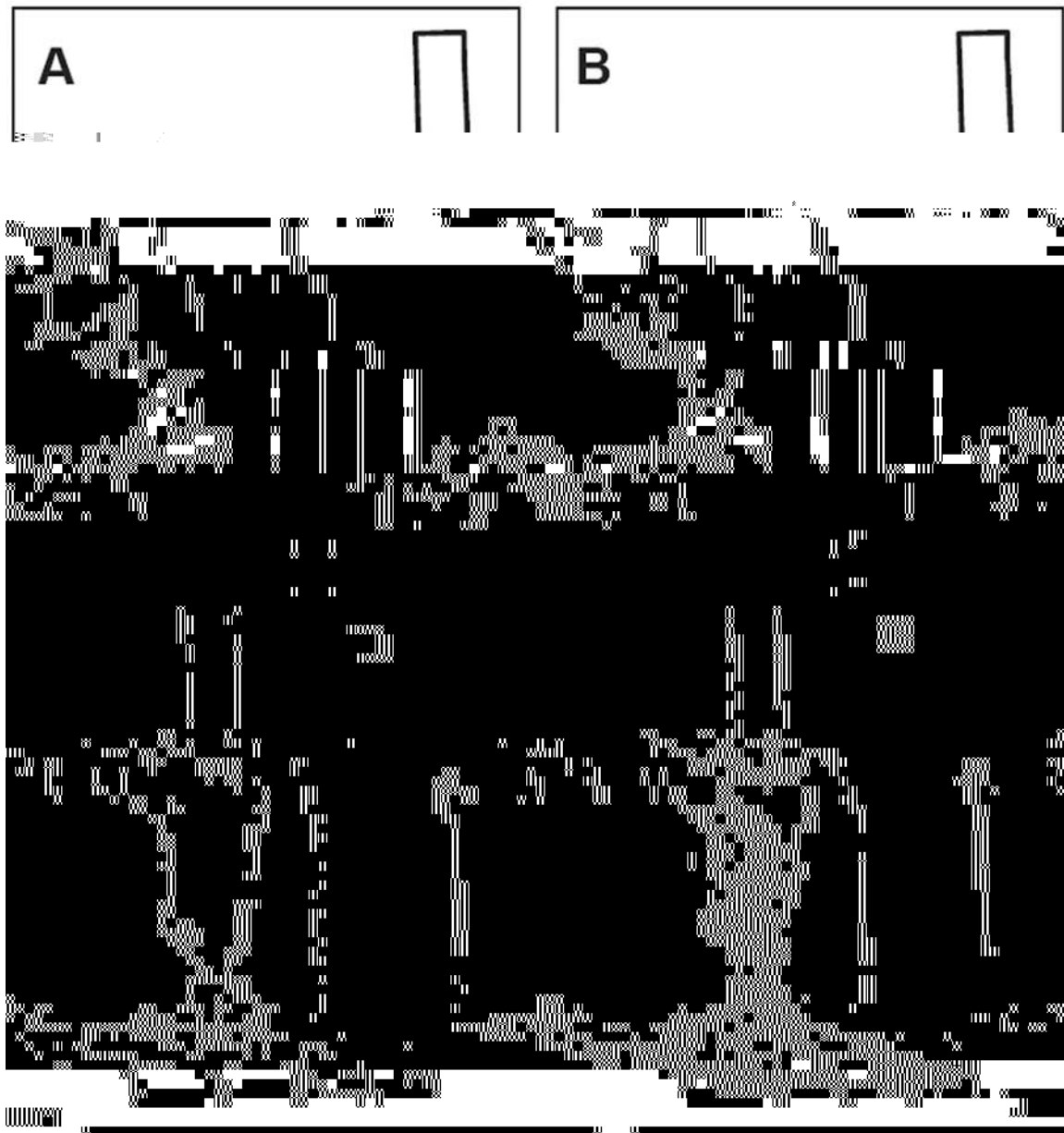


FIG. 6. Distribution of element types recorded at Konza Prairie Biological Station (KPBS) in 2006 for (A) *ci* element 1, (B) *ci* element 2, and (C) *ci* element 3. Thick black lines indicate approximate geographic boundaries between element types. The fourth map (D) shows the partial congruence of dividing lines between element types for all three *ci* 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 on song.**—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 =  $0.15 \pm 0.02$  [SE]; ASY: mean =  $0.14 \pm 0.02$ ;  $t = 0.1$ ,  $n = 10$ ).

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

(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

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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 10, 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 data, we observed a clear positive relationship between element dissimilarity and distance for the most common, *ch* element, DK# (Fig. 1). Bird pairs located



or elements are shared across dialects (Baptista 2000), there is both qualitative (Baptista 2000) and quantitative (Bell et al. 2000) variation within putative dialect areas, and dialect boundaries are not completely discrete (Baptista 2000). 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 1992, Tracy and Baker 1996); 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 2000, Slater 2000). We should point out, however, that only one of our three quanti-

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