CULTURAL EVOLUTION IN THE EURASIAN TREE SPARROW: DIVERGENCE BETWEEN INTRODUCED AND ANCESTRAL POPULATIONS[1]

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Abstract. We investigated cultural evolution in the song of the introduced North American population of the Eurasian Tree Sparrow (*Passer montanus*), derived from 12 pairs brought from Germany in 1870. These birds were liberated at St. Louis, Missouri, and spread into Illinois. Cultural evolution is described here in terms of the processes of population differentiation where the song meme was the unit of transmission. The distribution of song syllable memes in each meme pool fit a null hypothesis of a neutral model with an equilibrium between mutation, migration, and drift, indicating that the memes are functionally equivalent. The introduced and ancestral (German) populations showed marked divergence in the level of meme sharing. The small size of the founding North American population, the loss of genetic diversity there, and the relative susceptibility of meme pools to founder effects suggest that much of the reduction in sharing of syllable types occurred during the founding event. Because memes also are susceptible to extinction due to drift, memes were probably lost in both populations as a result of random memetic drift. Meme diversity in Illinois was comparable with that in Germany, suggesting a large mutational input into the former population following its founding. Estimates of mutational divergence based on the frequencies of song memes in meme pools showed more population structure in Illinois than in Germany. There also was less meme flow among meme pools in Illinois than in Germany. These results suggest that there were a series of founding events during the colonization of North America.

Key words: Eurasian Tree Sparrow, Passer montanus, song, cultural evolution, memetic differentiation.

INTRODUCTION

Studies of population differentiation often attempt to determine the relative importance of the various forces that cause and prevent population divergence. There is considerable interest in determining the genetic importance of one of these forces in particular: founder effects and their associated bottlenecks and drift. Theory suggests that bottlenecks affect pools of cultural traits in ways that are analogous to their effects on gene pools (Mundinger 1980, Cavalli-Sforza and Feldman 1981, Lynch and Baker 1993). In fact, bottlenecks often have been suggested as the cause of macrogeographic variation in bird song (Thielcke 1973, Baptista and Johnson 1982, Lynch and Baker 1994). However, bottlenecks in bird song rarely have been documented in natural populations (Baker and Jenkins 1987).

Populations introduced by humans are of interest to students of evolutionary biology because they are isolated from the homogenizing effect of the flow of genetic and cultural traits from the parent population. Because the date of introduction, the size, and the origin of such populations often are precisely known, inferences also can be made about the impact of microevolutionary forces on these populations. Although such introductions are relatively recent, high rates of cultural mutation allow cultural evolution to proceed even over short time intervals (Jenkins 1978, Ince et al. 1980, Lynch et al. 1989). To date, few studies have examined differentiation in song between introduced and parental populations of birds (Jenkins and Baker 1984).

The Eurasian Tree Sparrow *Passer montanus* (hereafter referred to as Tree Sparrow) is an ideal organism with which to study the applicability of models of cultural evolution to bird song. This species is native to much of Europe and Asia, and was introduced into North America when 12 pairs from Germany were released on

25 April 1870 at Lafayette Park, St. Louis, Missouri (Widmann 1889, Phillips 1928). The small size of the founding population suggests that a strong potential existed for founder effects to influence this population. This hypothesis is supported by St. Louis and Barlow (1988) who found a reduction in genetic variation in the introduced population.

Lang and Barlow (1987) discussed evidence for song learning in the Tree Sparrow and in the House Sparrow (*P. domesticus*). Cultural transmission of song in the Tree Sparrow also is suggested by the extensive variation found in song elements among the repertoires of individual males and populations of Tree Sparrows (Lang and Barlow 1987). Although cultural transmission of song has not been studied in detail in the Tree Sparrow, studies of a variety of species of oscines have shown that song elements are faithfully transmitted across generations, despite occasional mutations (Jenkins 1978, Payne et al. 1988, Trainer 1989).

In this report, we test the fit of the distribution of Tree Sparrow song elements to a null model in which song elements are selectively neutral and their distribution is due to an equilibrium among mutation, migration, and drift. We also describe the pattern of cultural differentiation that has developed between song pools of the introduced North American and ancestral German populations. We present data on song syllable sharing, flow, and diversity in the two populations that, given the history of the introduced population, are consistent with the influence of founder effects, drift, and frequent mutations.

MATERIALS AND METHODS

SONG STRUCTURE

The Tree Sparrow is a continuous singer (*sensu* Hartshorne 1956). We follow our original description of the structure of the song of this species (Lang and Barlow 1987) in giving the term syllable to the song elements that make up its continuous song. While singing, male Tree Sparrows group syllables into bouts that last as long as 10 min. Our operational definition of a bout is a group of syllables separated from adjacent groups by a time interval of greater than 2.5 sec (Lang and Barlow 1987). Each male has a repertoire of as many as 54 distinct syllable types that it uses in the nest-site song. Many of these syllable types are shared with other males (Lang

and Barlow 1987). The Tree Sparrow is semi-colonial (Summers-Smith 1988) and the territory defended by males is limited to the nest hole (Lang, unpubl. data). The nest-site song is used only in mate attraction. Males use a visual display (termed Kopfhoch-Drohen or head-up threatening by Deckert 1962) rather than vocalizations to repel other males that venture too close to the nest hole (Lang, unpubl. data).

SAMPLING

Tree Sparrow nest-site songs were recorded in the breeding season from April to July 1985 in Illinois near White Hall, Greene County (WH), Beverly, Adams County (BV), Meredosia, Morgan County (ME), and Jacksonville, Morgan County (JA) (see Lang and Barlow 1987), and in 1987 near Brussels, Calhoun County (BF), Loami, Sangamon County (LO), Industry and Fandon, McDonough County (MC), Havana, Mason County (HV), and again near Beverly, Adams County (Fig. 1). In Germany, songs were recorded in 1986 near Bockenem, Niedersachsen (NS), in Stuttgart (SG) and near Karlsruhe (KA) in Baden-Württemberg, and in 1988 near Haubersbronn, Baden-Württemberg (HA), and again near Bockenem, Niedersachsen (Fig. 1). An extensive sampling regime was followed in which efforts were made to sample the songs of as many localities as possible and to sample as large a portion of the songs of each locality as possible. Therefore, the songs of many males were taped at each locality. Because males use progressively smaller repertoires as their nesting cycles progress (Lang, unpubl. data), there is large variation in the repertoire sizes obtained from individual males (with a mean of approximately 10 syllable types). However, we assumed that the distribution of large and small repertoires was randomly distributed among samples obtained from the 12 localities. The date of sampling did not affect the distribution of repertoire sizes from each locality because Tree Sparrows raise two to three broods per breeding season in North America (Anderson 1978) and males in the early stage of the nesting cycle are present throughout the breeding season. Singing males were tape recorded until well after they began to repeat syllable types used in earlier song bouts. Sample sizes are given in Table 1. Recordings were made with a Uher 4000 Report IC tape recorder set at a tape speed of
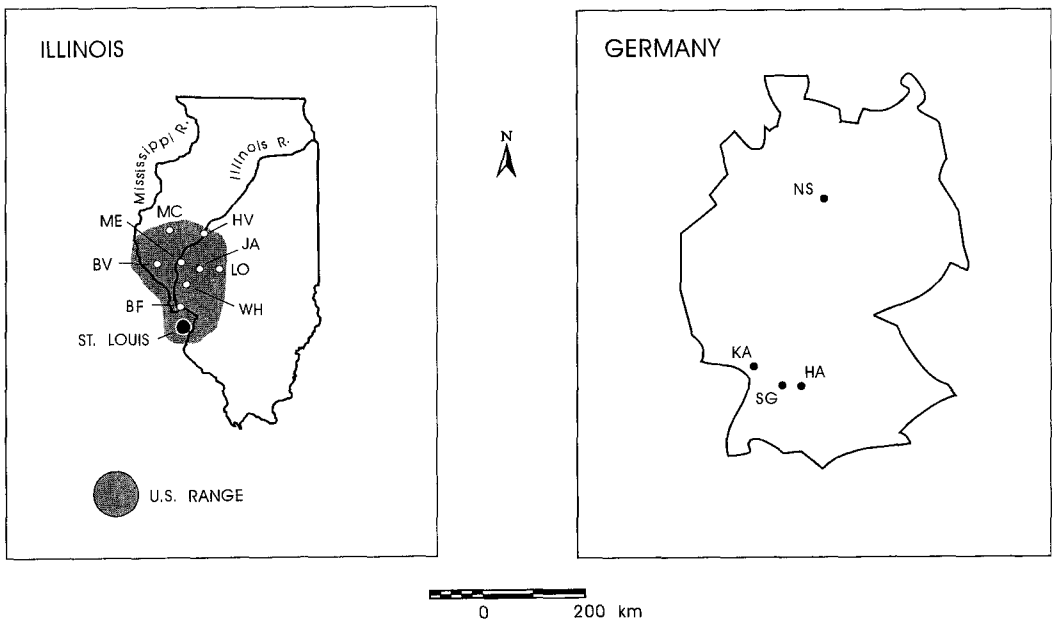
FIGURE 1.   Map showing sampling localities. See text for explanation of acronyms.

19 cm sec^{-1} or a Sony WM-D6C tape recorder with a Dan Gibson P-200 parabolic microphone.

ANALYSIS AND DEFINITIONS

Audiospectrograms of songs were made using a Kay Elemetrics Sona-Graph 7800 using a wide-band (300 Hz) setting and a frequency range of 80–8,000 Hz, a Unigon FFT Spectrum Analyzer, and a Kay 7900 printer or a Kay DSP Sona-Graph 5500 and Kay 5510 printer.

The sharing of syllable types among samples served as the basis for assessing the cultural divergence of the introduced North American population from the German population. Lang classified syllables into syllable types by visual assessment of their similarity (Marler and Pickert 1984, Slater et al. 1984, Lynch et al. 1989), and a pool of syllables was developed for each of the localities. Syllables were classified so that there was less variation within than among syllable types. Figure 2 illustrates this discontinuous variation in syllable morphology. Six similar syllables from five localities in Germany and Illinois are shown. These syllables were classified into two syllable types. Lynch and Baker (1986, 1994) and Lang and Barlow (1987) discuss the advantages of visually classifying songs over other methods. Birds also perceive song elements as falling into discrete categories; even

TABLE 1.   Number of birds tape recorded, syllables, syllable types, and private syllable types by locality and population.

Locality	No. birds	Total no. syllables	No. syllable types	No. private syllable types
Germany				
NS	44	380	203	78
KA	57	430	179	66
SG	58	536	204	68
HA	33	327	158	65
Total	192	1,673	503[a]	360[b]
Illinois				
BF	33	298	141	60
WH	37	292	169	50
BV	35	353	140	42
ME	58	346	162	45
JA	42	289	154	48
LO	28	299	139	61
MC	18	210	84	32
HV	44	312	144	59
Total	295	2,399	697[a]	554[c]
Grand total	487	4,072	1,057[a]	143[d]

[a] Syllable types occurring in more than one locality are included only once in totals.
[b] No. syllable types found in one or more German samples.
[c] No. syllable types found in one or more Illinois samples.
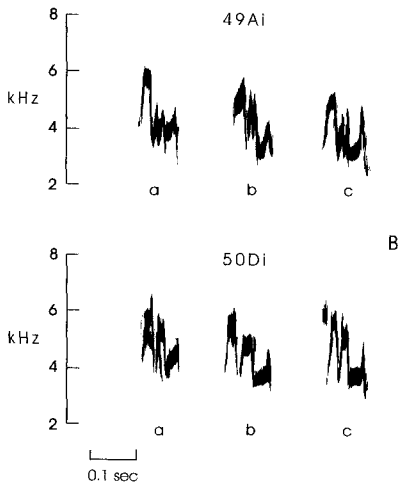[d] Number of syllable types shared between Illinois and Germany.

FIGURE 2. An example of the classification of Eurasian Tree Sparrow syllables into syllable types with less variation in syllable morphology within than among syllable types. A. Syllable type 49Ai. a. male no. M242, locality JA. b. male GM157, locality HA. c. male M77, locality ME. B. Syllable type 50Di. a. male GM2, locality SG. b. male M240, locality JA. c. male GM 120, locality NS.

elements that are continuously varying are categorized (Nelson and Marler 1989). In total, 4,072 syllables from 487 birds from four German and eight Illinois localities were classified into 1,057 syllable types. The large number of syllable types and the small mean number of syllables per syllable type that resulted from this classification are a result of three phenomena: (1) males of this species each have large repertoires of syllable types, (2) high rates of cultural mutation generate a large diversity of syllable types (Lynch et al. 1989, Lynch and Baker 1994), and (3) some males sang a small portion of their repertoires when they were taped. Therefore, the sampled repertoires of some of these males shared few syllable types with repertoires sampled from other males. Numbers of syllables and numbers of syllable types found in each locality are reported in Table 1. The numbers of syllable types restricted to only one sample also are listed. These are analogous to "private" alleles (Slatkin 1985) and thus are termed private syllable types.

We follow Dawkins' (1976) use of the term meme for any culturally transmittable trait, and Jenkins and Baker's (1984) definition of song meme as a culturally transmittable individual syllable or a group of linked syllables. Here we use the term meme to refer only to individual syllables. We refer to the pool of syllables sampled from a locality as a meme pool (Lynch et al. 1989).

POPULATION DIFFERENTIATION

The degree of differentiation among meme pools within a population can be estimated using a measure of mutational divergence (Lynch and Baker 1994). Latter (1973) defined this measure as:

$$\gamma = 1 - (I_B/I_W), \tag{1}$$

where I_B is the expected probability of identity among genes or memes drawn from different gene (meme) pools within that population, and I_W is the expected probability of identity of genes (memes) within a gene (meme) pool. Identity here is the probability that two randomly chosen memes are identical. γ is dependent upon mutational input and migration, but is independent of sample size in an island model of population structure and under a neutral model of differentiation (Lynch and Baker 1994). In an island model, migration is possible between any pair of gene (meme) pools. The probabilities of identity were calculated from the frequencies of memes in each meme pool (see Lynch and Baker 1994 for equations). Mutational divergence of song syllables was calculated for both the Illinois and German populations. All calculations were performed using a Turbo Pascal program written by A. Lynch.

The percentage of syllable types shared among samples was used to examine the relationships among the meme pools represented by these samples. A multivariate measure of dissimilarity (memetic distance) among meme pools was calculated following Lynch and Baker (1994). The presence (1) or absence (0) of a syllable in the meme pool of a locality was scored, resulting in a binary matrix. Jaccard's coefficient (Sneath and Sokal 1973) was used to calculate the level of syllable sharing among meme pools. The resulting similarity values were converted into distance measures (memetic distance) by taking their negative natural logs. Memetic distances then were used to reconstruct the relationships among meme pools. Neighbor-joining (Saitou and Nei 1987) and UPGMA cluster analyses, principal coordinate analysis, and multi-dimensional scaling (Sneath and Sokal 1973) were

performed on these distances using the NT-SYS package of statistical programs (Rohlf 1988). A minimum spanning tree was calculated using NT-SYS to connect the samples in principal coordinate space.

ESTIMATES OF MEME FLOW

Meme flow among meme pools within each of the two populations (Illinois and Germany) was estimated using Slatkin's (1985) rare alleles method. This method uses the frequencies of alleles restricted to one gene pool ("private" alleles) to indicate gene flow. The method assumes that these frequencies will be high when the level of flow among gene pools is low and that they will be low when the level of flow is high. Lynch et al. (1989) showed that this method can be applied to bird song memes. Flow is calculated using the formula:

$$\ln[\bar{p}(1)] = a[\ln(Nm)] + b, \qquad (2)$$

where $\bar{p}(1)$ is the mean frequency of alleles (memes) restricted to one gene (meme) pool, and a and b are constants (Slatkin 1985). The resulting value of Nm is an estimate of the number of genes (memes) per generation that are derived from migrants.

MEME DIVERSITY

Meme diversity of samples was calculated using the method of Lynch and Baker (1993). They applied the Kimura and Crow (1964) infinite alleles model to memes, in which memes belong to a single locus with infinite alleles. The model assumes that each mutation creates a new meme that is different from previous memes. Given the large number of memes found in Tree Sparrow song samples (Table 1), the probability that two memes (syllables) are similar due to convergence is probably low, especially when the short time that the German and Illinois populations have been separated is taken into consideration. Therefore, this model seems appropriate. To calculate meme diversity, Lynch and Baker (1993) used an estimate of meme identity from population genetics and calculated its inverse. The resulting value is known as the effective number of alleles (Kimura and Crow 1964):

$$\hat{s}_e = 1/\hat{\imath}, \qquad (3)$$

where $\hat{\imath}$ is an unbiased estimate of meme identity. Identity estimates were calculated from the frequency of each syllable type in each sample

(see Lynch and Baker 1993 for equation). $\hat{s}_e$ is here termed the effective number of memes. $\hat{s}_e$ represents the number of different memes that would exist in an ideal population in which all memes have equal frequency. The value of $\hat{s}_e$ can range from 1 (only one meme) to a value equal to the number of memes in the population (an even frequency distribution) (Lynch and Baker 1993). Confidence intervals of diversity estimates were calculated using the delete-half jackknife resampling procedure (Wu 1986). A frequency distribution of diversity estimates was obtained and the 2.5th and 97.5th percentiles were used as the 95% confidence limits. For each sample, 1,000 replicates were performed. Both $\hat{s}_e$ and the confidence intervals were calculated using a Turbo Pascal program written by A. Lynch.

TESTS OF NEUTRALITY

The distributions of song elements in populations of several species of birds conform to a neutral model (Slater et al. 1980, Lynch and Baker 1993, Lynch 1996). This suggests that the distributions of memes in these species are not due to selection but to random processes. To test the neutrality of memes in the Tree Sparrow, we used Lynch and Baker's (1993) method to compare the observed distribution of meme frequencies with the distribution expected in a neutral, infinite alleles model. Lynch and Baker (1993) used Ewens' (1972) maximum likelihood method to generate the expected distribution of meme frequencies. Ewens (1972) showed that this distribution could be estimated from the total number of distinct memes, s, in a sample and the size of the sample, n. Following Watterson (1978), Lynch and Baker (1993) compared the observed and expected values of I to test the fit of the observed distribution of meme frequencies to that expected under a neutral model. The observed value of I can be calculated as above, and the expected value can be obtained using the equation:

$$E(I) = 1/(\theta + 1), \qquad (4)$$

where $\theta = 2N_e\nu$ and is derived from Ewens' (1972) maximum likelihood method (Lynch and Baker 1993). ν is the combined effect of mutation (μ) and migration (m) rates. Lynch and Baker (1993) calculated the expected values of I by simulation and obtained confidence limits from the resulting distribution. We calculated the

TABLE 2. Among-meme pool differentiation (γ), mean frequency of private syllables ($\bar{p}$ [1]) and standard error (SE), and estimates of meme flow (*Nm*) among meme pools.

Population	γ	$\bar{p}$ (1)	$\pm$SE	*Nm*
Illinois	0.767	0.00599	±0.00022	34.03
Germany	0.689	0.00461	±0.00021	87.83

observed and expected value of *I* for each of the samples using a Monte Carlo simulation performed by a Turbo Pascal program written by A. Lynch.

RESULTS

POPULATION DIFFERENTIATION AND MEME FLOW

The two populations differed in their degree of population structuring. There was more mutational divergence among the Illinois meme pools than among the German meme pools (Table 2). Levels of meme flow among meme pools were consistent with levels of differentiation, being lower among meme pools in Illinois than in Germany (Table 2).

The results of the principal coordinate analysis are shown in Figure 3. This analysis was based on memetic distances (Table 3). The first three axes accounted for 61.6% of the variation (axis 1: 34.4%, axis 2: 14.8%, axis 3: 12.4%). The plot shows a greater degree of sharing of syllable types among meme pools within the parental and introduced populations than between the two populations. The divergence between the two populations was so great that few syllable types are presently shared (Table 1). The eight Illinois meme pools separated from the four German meme pools on the first axis of the principal coordinate analysis. Although Illinois and German meme pools are not separated on the second and third vectors, the minimum spanning tree suggests that the Illinois meme pools are most similar to each other and that each German meme pool is most similar to other German meme pools. Multidimensional scaling gave a similar result.

Results of cluster analysis of memetic distances were similar to those from the principal coordinate analysis. Figure 4 shows the results of clustering using the neighbor-joining method,
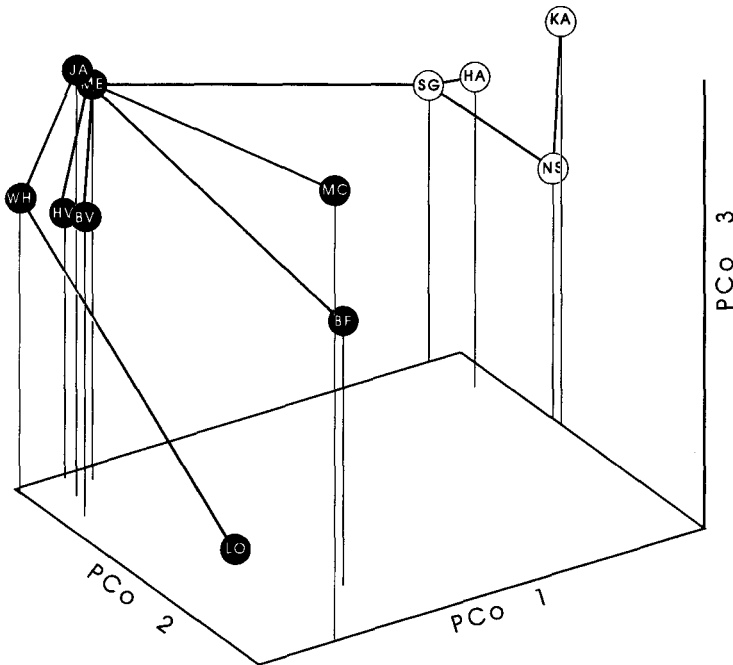

FIGURE 3. Three-dimensional principal coordinate solution and minimum spanning tree based on memetic distances among Illinois and German meme pools. Closed circles represent samples of memes from Illinois localities and open circles are samples from German localities. See text for explanation of acronyms.

TABLE 3. Memetic distances among German and Illinois samples.

	KA	NS	HA	SG	WH	JA	ME	BV	BF	HV	LO
Karlsruhe											
Niedersachsen	1.622										
Haubersbronn	2.155	1.759									
Stuttgart	1.625	1.589	1.720								
Whitehall	3.100	2.767	2.786	2.511							
Jacksonville	2.601	2.879	2.736	2.547	1.458						
Meredosia	2.627	2.610	2.558	2.312	1.488	1.390					
Beverly	2.941	2.680	2.937	2.785	1.822	2.002	1.742				
Brussels	2.708	2.546	2.748	2.593	2.350	2.295	2.325	2.371			
Havana	2.890	3.030	2.819	2.648	2.072	2.153	2.047	2.295	2.697		
Loami	3.006	2.677	2.934	2.730	2.303	2.561	2.492	2.458	2.414	2.425	
McDonough	2.737	2.898	2.953	3.136	2.511	2.389	2.321	2.565	2.327	2.653	2.703

and reveals divergence between Illinois and German meme pools. UPGMA gave results that were virtually identical in topology to those from the neighbor-joining method, but because the neighbor-joining method does not assume equal rates of evolution on all branches, only results from the latter are illustrated. Identical trees were obtained whether the tree was rooted at the midpoint or using the German meme pools as outgroups. This tree shows slightly longer branch lengths for the Illinois meme pools than German meme pools (Fig. 4). When untransformed memetic distances were used in various ordination and clustering methods, virtually identical results were obtained.

MEME DIVERSITY

In general, meme diversity in Illinois meme pools was not significantly different from that of German meme pools, despite some variation in diversity estimates among the meme pools. This
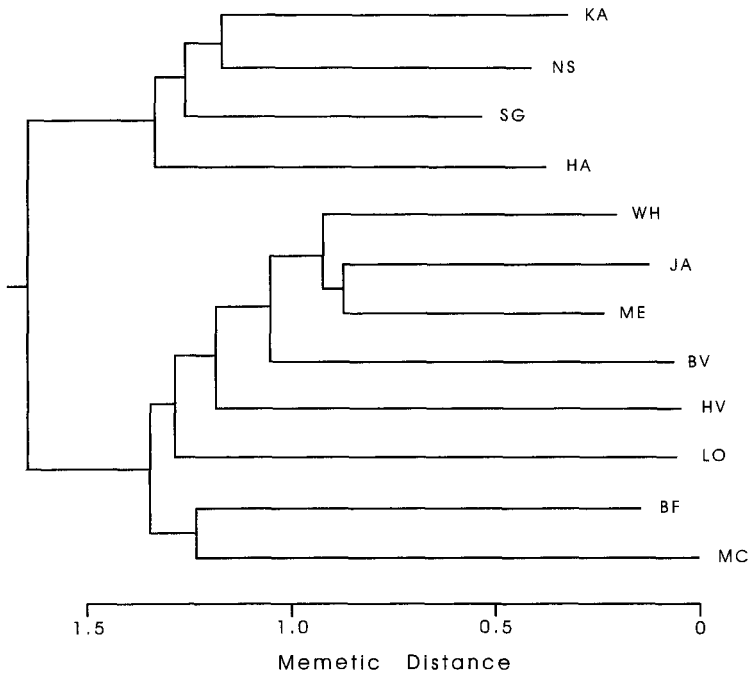

FIGURE 4. Neighbor-joining cluster analysis of memetic distances among Illinois and German meme pools (cophenetic correlation: $r = 0.82$, $P = 0.001$).
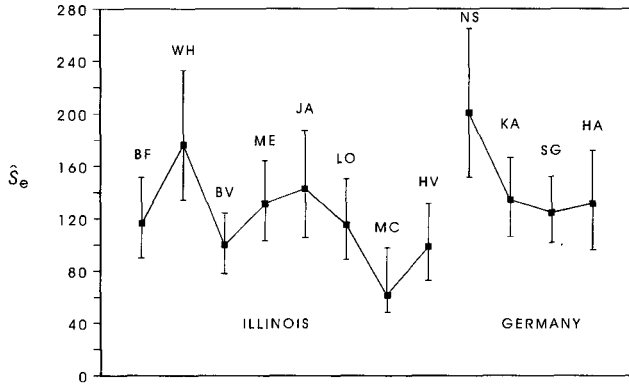
FIGURE 5. Meme diversity by meme pool, where meme diversity is measured by the effective number of memes ($\hat{S}_e$); see text for details.

is illustrated by overlap in 95% confidence limits (Fig. 5).

TESTS OF NEUTRALITY

There was good agreement between the observed and expected values of I in each of the meme pools (Table 4). This suggests that within-meme pool variability was primarily neutral and that the distribution of memes is a result of input from immigration and mutation and elimination of memes due to random extinction.

DISCUSSION

The meme pools of the North American population of the Tree Sparrow have diverged considerably from those of the German population. This divergence is manifested in the dramatic loss of shared syllable types in the 115 years between the introduction of this species to North America and our sampling (Table 1). This divergence is probably largely due to founder effects as suggested by the small size of the founding population, genetic evidence (St. Louis and Barlow 1988), and cultural evolutionary theory (Cavalli-Sforza and Feldman 1981, Lynch and Baker 1994). Although St. Louis and Barlow (1988) did not detect a reduction in mean heterozygosity in the Illinois population, they found a small but statistically significant reduction in the mean number of allozyme alleles per locus (St. Louis and Barlow 1991). Experimental manipulation of population size in fish by Leberg (1992) showed that the latter is a more sensitive indicator of bottlenecks. St. Louis and Barlow (1988) attributed the reduction of genetic diversity in the Illinois population to founder effects and genetic drift as a result of the small size of the founding population. Therefore, there was a high potential for the meme pool to have undergone founder effects and drift as well. A loss of syllable types as a result of founder effects would account for the observed lack of syllable type sharing between Illinois and Germany. Results from cluster analysis using the neighbor-joining method suggest that drift immediately following the founding event also had an impact on the Illinois population. Longer branch lengths for Illinois meme pools suggest more rapid divergence as a result of drift than in Germany (Fig. 4). Despite drift in the parental German population, a loss of syllable types of the same magnitude probably did not occur there because of replenishment of lost syllable types via meme flow from adjacent European populations. The action of drift on bird song has been implicated by other studies of isolated populations of birds

TABLE 4. Observed ($\hat{I}$) and expected [E(I)] meme identity within meme pools.

Locality	$\hat{I}$	E(I)	95% CL
NS	0.0050	0.0051	0.0043–0.0064
KA	0.0074	0.0076	0.0059–0.0105
SG	0.0080	0.0085	0.0069–0.0101
HA	0.0078	0.0078	0.0063–0.0101
BF	0.0086	0.0094	0.0073–0.0176
WH	0.0056	0.0063	0.0051–0.0077
BV	0.0099	0.0113	0.0090–0.0195
ME	0.0074	0.0087	0.0069–0.0107
JA	0.0068	0.0078	0.0062–0.0092
LO	0.0084	0.0099	0.0079–0.0133
MC	0.0155	0.0193	0.0143–0.0283
HV	0.0104	0.0099	0.0075–0.0125

(Bitterbaum and Baptista 1979, Baker and Jenkins 1987, Lynch and Baker 1994).

The divergence between the Illinois and German populations also is probably characterized by the creation of a large number of syllable types due to mutation. Both the finding that levels of diversity in Illinois are comparable with that of Germany and the presence of a large number of private syllable types in the Illinois population (Table 1) suggest that a high mutation rate restored diversity in Illinois. This finding is consistent with Lynch and Baker's (1994) prediction that meme diversity would rapidly recover following a founding event due to the high mutation rates that have been observed for memes (Jenkins 1978, Slater and Ince 1979, Lynch and Baker 1994). Together, these results, as well as the loss of genetic variation in the Illinois population, suggest that the divergence of Illinois meme pools from German meme pools was due primarily to both the loss of a large number of syllable types during the founding of the Illinois population and to a large mutational input.

Our results are consistent with theory that suggests that syllable types are highly susceptible to loss due to founder effects. This is a result of syllable types generally occurring at low frequencies and subsequently having very high diversity (Lynch et al. 1989, Lynch and Baker 1994). These low frequencies also are evident among Tree Sparrow syllable types as can be seen in Table 1 where the number of syllable types is large relative to the number of syllables. This low average frequency and high diversity arises in part from the large population size for memes (Lynch et al. 1989, Lynch and Baker 1994). For example, each male Tree Sparrow can potentially carry over 50 distinct syllable types, as opposed to only two copies of each gene locus. The high rates of mutation typical for memes also contribute significantly to the high diversity and hence the low frequencies seen for syllable types (Lynch et al. 1989, Lynch and Baker 1994). Therefore, a small group of birds selected to found a population is likely to carry syllable types that are representative only of a very small area of the ancestral population, whereas their allozymes would be representative of a much larger area. As an example, consider a hypothetical sample of 30 birds each with a repertoire of 10 syllable types. This represents a meme pool size of 300 syllables. If each of these 30 males sang a copy of the same syllable type,

then 10 per cent of the meme pool would be composed of that syllable type. This represents the maximum percentage that could be attained by a syllable type in this sample. Because many syllable types are not shared by all males in samples of Tree Sparrow song, such syllable types have even lower frequencies. For example, in the WH meme pool, syllable types range from 0.3 to 2.4% of the sample with a mean of 0.6%. In contrast, most allozyme loci in Tree Sparrow samples have only one or two alleles, and therefore most alleles are not rare (St. Louis and Barlow 1988). Founder effects acting on such samples would result in the loss of only the few rare alleles, but many syllable types. Syllable types also probably are prone to extinction due to drift for the same reasons that they are easily lost to founder effects (Lynch et al. 1989, Lynch and Baker 1994).

The present results suggest that the Illinois population also differs from the German population in that colonization events in the introduced population appear to have resulted in greater population structuring in Illinois than in Germany. Although levels of meme diversity in Illinois meme pools are comparable with those of meme pools in Germany, there is less sharing of syllable types among meme pools in Illinois than in Germany. This is reflected in a greater level of mutational divergence (γ) and lower rate of meme flow among Illinois meme pools. These results suggest that there were several founding events and subsequent drift as small groups of birds from the recently founded Illinois population colonized new areas, and that there has not been enough time for meme flow to bring levels of syllable type sharing among meme pools up to those found in Germany. Longer branch lengths for Illinois meme pools in the neighbor-joining tree may be due in part to such effects.

Bottlenecks in the total size of the North American population size following the initial colonization event probably did not occur and therefore would not have played a role in the reduction in overall syllable sharing between Illinois and Germany. The Illinois population appears to have grown rapidly shortly after release (Merrill 1876, Widmann 1889). As discussed above, some Illinois meme pools may have lost more syllable types through individual founder effects and drift than did German meme pools. However, these syllable types were likely pres-

ent in other Illinois meme pools. This would have prevented further net reduction in syllable sharing with Germany. Although testing of alternative hypotheses to explain the divergence of Illinois and German meme pools was beyond the scope of this study, two hypotheses would be worthy of investigation. Lynch and Baker (1993) suggested that colonization by juveniles that have not completed song learning ("withdrawal-of-learning;" Thielcke 1969, 1973) could cause an initial reduction in meme diversity in a founding population. However, Illinois meme pools shared approximately 14% of their syllable types with German meme pools and the remaining Illinois syllable types are similar to German syllable types, suggesting that the founders of the Illinois population had learned the species typical song. There may be differences in the acoustical environments of Illinois and Germany that also could have an impact on the composition of meme pools. However, the habitat occupied by Tree Sparrows in the two areas at the present time appears similar. In both areas, this species inhabits riparian woods with little understory, large city parks with scattered, large trees and grass, orchards, and farmyards. Although the acoustical environment might influence gross time and frequency characteristics of syllables, it is not known how this affects the microstructure of syllables (Lynch and Baker 1993).

In conclusion, the results of this study implicate the effect of the history of the introduced population on the distribution of the syllable types within it. There was considerable divergence between Illinois and German meme pools. This divergence is consistent with the predictions of a neutral model with random extinction of memes due to founder effects and drift, input of memes from a high mutation rate, and curtailed migration between the populations. The small size of the founding Illinois population facilitated an initial loss of many syllable types. The high rate of mutation inherent in cultural traits allowed a subsequent recovery of syllable diversity in Illinois and introduced many new syllable types into the population. Although models of nonrandom processes have not been tested, we have tested the fit to a neutral model and failed to reject this null hypothesis. This is an important first step. However, tests of models of nonrandom processes deserve attention. Direct longitudinal studies of cultural transmission

also are important. These can corroborate the findings of the indirect methods used here.

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