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Population Memetic Analysis of Variation of Song, Geographical Distribution and Bill Morphology in the Reed Bunting

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We applied population memetic models to the analysis of cultural variation among 11 European reed bunting (*Emberiza schoeniclus*) populations belonging to two subspecies groups differing in bill morphology. We tested whether patterns of meme diversity within and among populations and between the two subspecies groups correspond to patterns of variation in bill morphology. Within-population meme diversity was high and the degree of memetic divergence within groups was significant and higher among southern thick billed populations than among northern thin billed populations. There was, however, no significant memetic difference between the two subspecies groups. Tests of correlation between all groups indicated that memetic variation is associated with geographical distance and not with morphological variation. The results suggest a demographic structure of reed bunting populations similar to that of island populations of other bird species. The lack of memetic differences between them indicates that populations are not culturally isolated, despite the morphological, ecological and genetic differences. We discuss possible evolutionary explanations of the patterns of variation found.

Keywords: *Emberiza schoeniclus*, cultural evolution, syllable types, AMOVA, Mantel tests

1. Introduction

Song in many songbird species is socially learned and, therefore, can be considered a "replicator" in a cultural evolution context, equivalent to genes, which are replicators in the context of biological evolution (Dawkins, 1976; Mundinger, 1980; Williams, 1992). In other words, the definition of "meme" (Dawkins, 1976) can be applied to songs or song elements (Lynch et al., 1989). The evolution of such memes, units of cultural transmission, can be investigated with tools borrowed from the study of population genetics and evolution assuming that there are parallels between the processes of cultural and biological evolution (Mundinger, 1980; Cavalli-Sforza and Feldman, 1981; Lynch, 1996). Both these processes can be defined as the change in frequency of traits in a population through differential transmission across generations, driven by analogous forces of mutation, selection, drift and migration (e.g. Payne et al., 1988; Lynch et al., 1989; Gibbs, 1990; Lynch and Baker, 1993, 1994; Payne and Payne, 1993; Beecher, 1996; Lynch, 1996; Payne, 1996; Burnell, 1998).

Lynch and Baker (1993, 1994) and Lynch (1996) derive measures of song meme differentiation and estimates of mutation and migration rates in bird populations to describe their histories using population genetics models. Another method useful to estimate cultural differences between populations is to compare population meme pools using indexes based on presence/absence of individual memes, from which cultural distance matrixes can

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be computed (Lynch and Baker, 1986; Baker and Jenkins, 1987).

These methods have been applied to the study of meme variation in chaffinch (*Fringilla coelebs*) populations on islands and mainland and in situations of recent and documented colonisation. Through memetic analysis, different authors have been able to estimate meme flow and mutation and to describe patterns of island colonisation (Slater and Ince, 1979; Lynch and Baker, 1986; Lynch et al., 1989; Lynch and Baker, 1993, 1994).

A similar population memetics approach, but with slightly different methods, was recently applied to the study of cultural variation in the song of the savannah sparrow (*Passerculus sandwichensis*) in coastal California (Burnell, 1998). Here, populations are not on islands, but live in fragmented salt marsh environments and are therefore somewhat isolated. The results are similar to the chaffinch case; a series of founder events, followed by mutation and occasional convergence, are argued to have given rise to the observed pattern of meme diversity (Burnell, 1998). Founder effects are thought to have determined meme pool composition also in island populations of singing honeyeaters (*Meliphaga virescens*; Baker, 1996).

Lynch (1996), after formalising the model of population memetics, illustrated the application of the method to different situations using data from a number of different species in other studies. He obtained measures of within population diversity, where the neutral model of meme evolution holds and where mutation and migration rates are approximately balanced, and of among population meme diversity, where he was able to estimate migration and mutation rates and degree of divergence of memes in different species.

In all the above cases the memetic divergence of populations is thought to be the result of chance events following their geographical isolation. If such isolation is sufficiently prolonged, the populations may diverge in ecology and, possibly, morphology, since geographical separation is thought to be the primary step in speciation processes in birds (Grant and Grant, 1997). There will then be a turning point where cultural divergence may be accelerated, upon secondary contact between the populations, because of the species recognition function of song and its role as a reinforcement to reproductive isolation (Baptista and Trail, 1992; Grant and Grant, 1997). Theoretically, given the high rates of meme mutation (Lynch, 1996), the point of accelerated cultural divergence could be reached in a relatively short time following isolation, possibly faster than genetic divergence (Cavalli-Sforza and Feldman, 1983).

The population memetics approach to the analysis of cultural variation, in species where geographical distance is coupled to ecological differences, can give insight to both evolutionary mechanisms and the role of song in speciation processes. The reed bunting (*Emberiza schoeniclus*) is a good model for investigating the role of cultural variation in population dynamics. This species is highly polymorphic in bill size and shape (Cramp and Perrins, 1994; Byers, 1995) and such polymorphism seems to be related to winter diet differences (Isenmann, 1990; Hillcoat, 1994). The two western European groups of subspecies, a “northern” migratory thin-billed group and a “southern” resident thick-billed group, have songs differing in quantitative features and the differences in song among populations are related to bill morphology more than to geographical distance (Matessi et al., 2000a). Genetic analyses suggest that the two groups have diverged recently and now could be in secondary contact (Grapputo et al., 1998). There is evidence for a possible narrow hybrid zone along the border of the breeding ranges, at least along the Alps, even though parapatric differentiation cannot be excluded (Brichetti and Cova, 1976; Grapputo et al., 1998; Matessi et al., 2000a). The species has a discontinuous distribution and populations in both breeding ranges are rather isolated and small due to the fragmentation of the preferred habitats (Nicholson, 1994), conditions that increase the differentiating effects of drift (Burnell, 1998).

In this study we investigate the influence of cultural evolution on processes of population dynamics and speciation. In particular, we apply the population memetics approach to the analysis of song variation to test if patterns of meme diversity within and among populations and between the two subspecies groups of reed buntings correspond to patterns of bill morphology variation. Given the recent divergence of bill morphs (Grapputo et al., 1998) and the moderate differences in song properties between morphs (Matessi et al., 2000a), a potentially more plastic marker, the shape of song syllables, could be expected to diverge more strongly and better reflect the division of populations according to bill morphology.

2. Methods

We recorded as many males as possible from seven populations of the northern group of subspecies and from four populations of the southern group of subspecies of reed bunting (Table 1, Fig. 1), between 1996 and 1998 (for details see also Matessi et al., 2000a). Individuals were not colour-ringed. We recorded at least 15 repetitions of song from each male with a 70 cm diameter parabolic reflector fitted with a Sony ECM-T140 omni-directional microphone and a Philips DCC170 tape recorder. The English recordings were provided by the British National Sound Archive, the recordings from Pusiano were provided by Enrico Viganò, some of the recordings from Busatello were provided by the Nisoria Ornithological Group and some of the recordings from Cerknica were provided by Tomi Trilar of the Ljubljana Natural History Museum. The recordings were processed with Avisoft SAS-Lab software; since within individual variability was low, we chose the song with the highest signal to noise ratio and the most complete sequence from each individual.

FIG. 1. Map of sampled reed bunting populations. Populations are: 1. England; 2. Munchhausen; 3. Radolfzell; 4. Magadino; 5. Pusiano; 6. Brabbia; 7. Cerknica; 8. High Adriatic; 9. Busatello; 10. Campotto; 11. Ebro Delta. Solid circles are northern subspecies group populations, open circles are southern subspecies group populations. The line represent the approximate boundary of the reproductive distributions of the two subspecies groups in western Europe

We printed sonograms with 223 Hz bandwidth, 0.0029 sec time resolution (Beecher, 1988) for each different syllable in each song and created a syllable catalogue. Syllables were then visually classified into types (Fig. 2). The classification criterion was overall similarity of shape of the sonogram trace and mean frequency shifts of

TABLE 1

Summary of information on the reed bunting populations analysed for memetic variation

Group	Locality	Subspecies	N	Bill	Position	Source of songs
Northern	Magadino	schoeniclus	9	5.2^a	46º10'N 8º52'E	this study
	Radolfzell	schoeniclus	10	5.08^a	47º44'N 8º59'E	this study
	Munchhausen	schoeniclus	10	5.3^b	48º44'N 7º54'E	this study
	England	schoeniclus	12	5.25^b	51º51'N 1º39'W	British National Sound Archive
	Brabbia	schoeniclus	11	5.46^a	45º48'N 8º42'E	this study
	Pusiano	schoeniclus	10	5.27^a	45º49'N 9º17'E	Enrico Viganò
	Cerknica	schoeniclus	9	5.33^a	45º47'N 14º23'E	this study, Ljubljana Natur. Hist. Museum
Southern	High Adriatic	intermedia	10	6.34^a	45º44'N 13º31'E	this study
	Busatello	intermedia	12	6.34^a	45º7'N 11º4'E	this study, Nisoria Ornithological Group
	Campotto	intermedia	10	7.0^a	44º36'N 11º51'E	this study
	Ebro Delta	witherbyi	13	6.3^a	40º42'N 0º48'E	this study

Note: Subspecies group (according to Byers et al. (1995)), number of individuals recorded, average bill height of males (mm), geographical position and sources of data are given. Source of bill size measurement: a) local ringing data, b) literature.

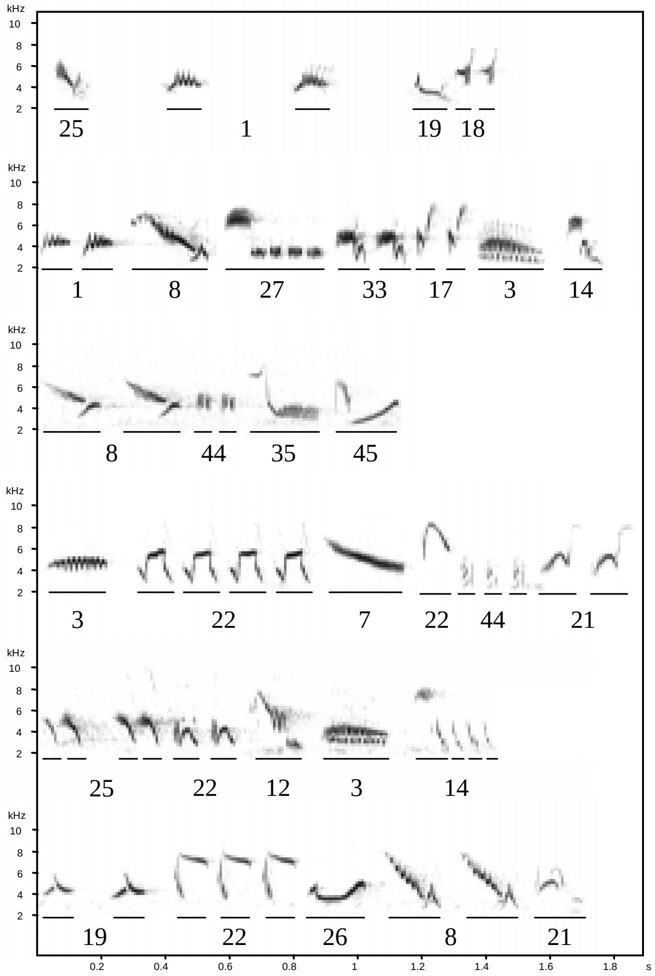

FIG. 2. Sonograms of songs of six individuals from different populations of reed bunting illustrating examples of syllable type classification

± 1.0 kHz were tolerated. The classification was then validated by two independent observers who were asked to form similarity groups in a subsample of 30 syllables belonging to 6 types. These were the types which included the largest number of syllables. Five syllables within each of these types were then randomly chosen for the validation. The observers correctly classified 93% and 97% of the syllables respectively. Within each syllable type different syllable variants could be recognised. Even though analyses at syllable variant level suffer less from classification biases in general (Lynch et al., 1989), reed bunting syllables were so different that most variants were present only once, therefore analyses were carried out only at the syllable type level (see also Lynch and Baker, 1994).

We analysed within-population meme diversity using one-, two- and three-syllable memes (Lynch et al., 1989; Lynch and Baker, 1993). Two- and three-syllable memes are defined as a sequence of two (three) different syllable types (repeats of a type are ignored) considered as a single block, i.e. transmitted as a unit. The same types, in a different order, are considered a different meme. We calculated and compared population indexes of meme diversity for all three meme types. First we calculated, for each population, the within – population probability of identity of memes (*I*) (i.e. the probability that two randomly chosen memes are identical):

$$I = \frac{v\sum_{k=1}^{t}(x_k^2 - 1)}{v - 1}$$

where ν = sample size of the population, *t* = total number of memes in the population and *x* = frequency of the k^{th} meme. From these we calculated the effective number of memes $s_e = 1/I$ (Lynch, 1996).

The population structure in our study was similar to a nested design analysis because we needed to compare populations both within subspecies groups and between subspecies groups. We therefore adapted the formulas given by Lynch (1996) accordingly. The population structure analyses were conducted using single-syllable memes only. We estimated the among-population memetic differentiation by calculating mutational divergence indexes:

$$\gamma_0 = 1 - \frac{I_{BW}}{I_W} \qquad \text{and} \qquad \gamma_1 = 1 - \frac{I_B}{I_W}$$

where γ_0 represents meme differentiation among populations within morphological groups and γ_1 represents the global meme differentiation among populations, regardless of morphological groups. In the above formulas, I_W is the average within-population meme identity (*I*):

$$I_W = \frac{1}{d}\sum_{i=1}^{d} I_i$$

with d = total number of populations and I_i = meme identity within population i;

$$I_{BW} = \frac{1}{n(n-1)+s(s-1)}$$

$$\left[\left(\sum_{i\neq j}^{n}\sum_{k=1}^{t} x_{ik}x_{jk}\right)+\left(\sum_{i\neq j}^{s}\sum_{k=1}^{t} x_{ik}x_{jk}\right)\right]$$

is the average meme identity among populations within subspecies group, with n = number of northern group populations, s = number of southern group populations, $x_{ik}x_{jk}$ = product of the frequencies of meme k in populations i and j, with $i \neq j$, and

$$I_B = \frac{1}{(n+s)(n+s-1)}$$

$$\left[\left(\sum_{i\neq j}^{n}\sum_{k=1}^{t} x_{ik}x_{jk}\right)+\left(\sum_{i\neq j}^{s}\sum_{k=1}^{t} x_{ik}x_{jk}\right)+2\left(\sum_{i=1}^{n}\sum_{j=1}^{s}\sum_{k=1}^{t} x_{ik}x_{jk}\right)\right]$$

is the index of meme identity among all populations, regardless of group membership, with $n + s = d$. If the two subspecies groups share less memes than the populations within the groups the third sum of products in I_B will be close to zero, thus $I_B < I_{BW}$, the memetic diversity between the subspecies groups will be higher than the average memetic diversity within them and the ratio of the two divergence indexes (γ_1/γ_0) will be much larger than one in absolute value.

We then proceeded to calculate estimates of meme flow per generation using the private memes method (Slatkin, 1985; Lynch, 1996). We calculated $N_e m$ = number of migrants per generation among all populations, among northern group populations, among southern group populations and between subspecies groups. To calculate the latter case, we used average frequency of memes present in the populations of only one of the subspecies groups. We applied Slatkin's correction to the calculated migrant values, as suggested by Lynch (1996). We used the relationship:

$$\phi = \frac{I_W - I_B}{1 - I_B} \approx \frac{1}{2N_e(m+\mu)+1}$$

to calculate the mutational inputs $N_e\mu$ corresponding to the migrational inputs at the different levels of analysis (Lynch, 1996).

In order to test the significance of memetic diversity within and between subspecies groups we applied standard population genetics F_{ST} analysis by estimating variation within each subspecies group separately and, pooling populations within subspecies group, by estimating variation between the groups. A nested design analysis of molecular (memetic) variance (AMOVA; Excoffier et al., 1992) allowed us to control for memetic variation among populations within the groups. We used meme frequencies as input for the Arlequin 1.1 population genetics analysis software package (Schneider et al., 1997), which was also used to perform neutrality tests and to calculate pairwise population memetic distances using the coancestry coefficient matrix (Reynolds et al., 1983; Schneider et al., 1997).

We obtained a matrix of distances between population meme pools by calculating the one-complements of the Jaccard index of similarity, a number between 0 and 1 which is based on presence/absence of memes and considers only simultaneous presence and not simultaneous absence as similarity between meme pools (Lynch and Baker, 1986).

Finally we tested the association of memetic, geographical and morphological distances between populations using Mantel tests of matrix correspondence. Pairwise geographical distances were calculated from exact locality co-ordinates (Table 1), except for the English population which was arbitrarily positioned in central southern England. Morphological distances were calculated using bill height measures from local ringing data or from the literature.

3. Results

We identified 59 syllable types that are present at least once in the whole sample, which represent the set of one-syllable memes. We found relatively high numbers of two- and three-syllable memes (266 and 186, respectively), most of which were found only once or in only one population, especially three-syllable memes.

TABLE 2

Memetic diversity indexes of reed bunting populations for memes of one, two and three syllables length

	One-syllable memes ($t = 59$)			Two-syllable memes ($t = 266$)			Three-syllable memes ($t = 186$)		
Population	m	I	s_e	m	I	s_e	m	I	s_e
Northern group									
Magadino	36	0.0302	33.2	21	0	∞	14	0	∞
Radolfzell	34	0.0303	33	19	0	∞	10	0	∞
Munchhausen	33	0.0417	24	21	0	∞	11	0	∞
England	28	0.0503	19.9	23	0.008	126.5	6	0	∞
Brabbia	47	0.0407	24.6	37	0	∞	25	0	∞
Pusiano	42	0.0418	23.9	30	0	∞	23	0	∞
Cerknica	27	0.0399	25.1	19	0	∞	9	0	∞
Southern group									
High Adriatic	32	0.0524	19.1	24	0.015	69	14	0	∞
Busatello	49	0.0383	26.1	40	0.0026	390	28	0	∞
Campotto	45	0.0343	29.1	32	0	∞	24	0	∞
Ebro Delta	51	0.0643	15.5	38	0.01	100	25	0.01	100

Note: m = total number of memes in the population, t = number of different memes, I = meme identity, $s_e = 1/I$ = effective number of memes.

Within-population meme diversity, measured by the effective number and the meme identity of single-syllable memes per population (s_e and I), did not differ between northern and southern subspecies group (Mann–Whitney U test: $U = 18$, $N_1 = 7$, $N_2 = 4$, $P = 0.45$). Multiple-syllable memes for most populations had zero meme identity values (I), and therefore practically infinite s_e (Table 2). Two-syllable meme identity (I) was marginally different between subspecies groups (Mann–Whitney U test corrected for ties: $U = 23$, $N_1 = 7$, $N_2 = 4$, $P = 0.05$). Of all populations only Ebro Delta had relatively low three-syllable memetic diversity (Table 2). The meme frequencies in all populations fit to a neutral infinite alleles model, after Bonferroni correction for the number of populations tested (Ewens–Watterson test of neutrality: all corrected $P > 0.05$).

The memetic differentiation among northern group populations was lower than that among southern populations ($\gamma = 0.382$ and $\gamma = 0.451$, respectively). The between subspecies group memetic differentiation was not higher than the within subspecies group differentiation, as estimated by the comparison of γ_0 and γ_1 ($\gamma_1/\gamma_0 = 0.4/0.416 = 0.961$). The number of migrant memes per generation at all population levels was considerably lower than the estimated mutation rates per generation (Table 3). The standard F_{ST} values, calculated considering meme frequencies equivalent to haploid allele frequencies input for population genetics analysis software, were significant within northern and within southern subspecies ($F_{ST} = 0.014$, $P < 0.0001$ and $F_{ST} = 0.021$, $P < 0.0001$, respectively) and between subspecies (populations pooled within group, $F_{ST} = 0.003$, $P = 0.02$). The nested AMOVA

TABLE 3

Population memetic parameters of reed bunting populations

	Memetic differentiation (γ)	Migrants per generation ($N_e m$)	Mutants per generation ($N_e \mu$)
Southern group	0.451	5.2	17.1
Northern group	0.382	7.4	24.5
All populations (γ_1)	0.4	8.7	19.7
Between groups (γ_0)	0.416	5.4	21.9

Note: Parameters for the all-populations level are calculated ignoring subspecies grouping.

TABLE 4

Analysis of memetic variance results using analysis of molecular variance (AMOVA) methods with meme frequencies (Excoffier et al. 1992, Schneider et al. 1997)

Source of variation	d.f.	*variance component*	% of variance	*p*
Between groups	1	0	0	0.53
Among populations within groups	9	0.008	1.7	<0.0001
Within populations	413	0.479	98.4	<0.0001

applied to meme frequency data shows that there is no significant memetic differentiation between northern and southern group, while there is significant variability among populations within groups and most of the variation (98%) is within populations (Table 4). The significance of the variance components is tested by a non-parametric test of 10000 permutations (Excoffier et al., 1992; Schneider et al., 1997). The nested design analysis, contrary to the previous one, takes into account the ‘among populations-within subspecies’ level of variation and is therefore a more reliable estimate of subspecies group memetic differentiation.

Cluster analysis of meme pool differences using the Jaccard index did not reveal a clear clustering of populations according to morphological group membership (Fig. 3A). Comparison of memetic distances using meme frequencies to calculate pairwise coancestry coefficients (Reynolds et al., 1983; Schneider et al., 1997) gave similar results (Fig. 3B). We tested the correlation between both memetic distance measures and morphological (i.e. bill height) and geographical distances among populations with Mantel tests of matrix correspondence. In both cases, memetic distance was significantly correlated to geographical distance and not to morphological distance (Jaccard index vs. geography: $r = 0.496$, $P = 0.006$; coancestry coefficients vs. geography: $r = 0.523$, $p = 0.005$) (Fig. 4).

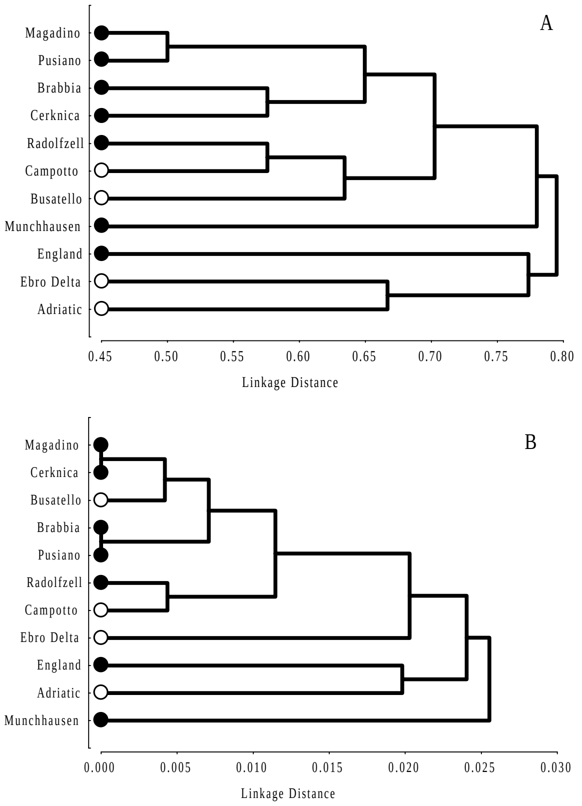

FIG. 3. Dendrograms from UPGMA cluster analysis of songs of reed bunting populations. A) Syllable pool distance (Jaccard index) and B) Meme frequency distance (coancestry coefficients). Solid circles = Northern populations, open circles = Southern populations

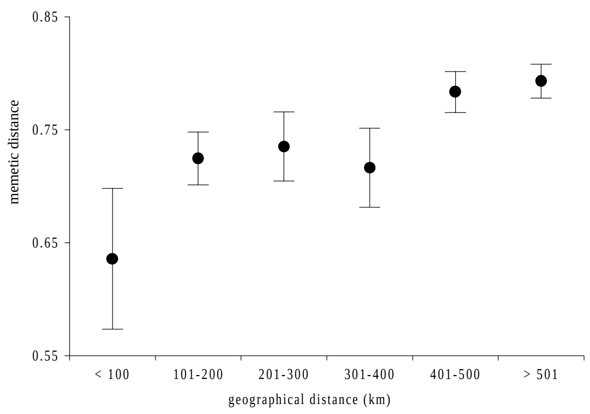

FIG. 4. Relationship between memetic distance (coancestry coefficients) and geographical distance (in 100-km classes) among reed bunting populations. Means ± S.E. are given for illustration purposes

4. Discussion

Contrary to what expected, we found no memetic variability associated with subspecies morphological groups. This result is confirmed by the memetic divergence indexes, the AMOVA results and the results of Mantel tests and is illustrated by the dendrograms. There is instead high memetic diversity within populations, especially for multisyllable memes, and high variability among populations in general. This is evident from the effective number of memes (s_e) values and from the highly significant among – populations term in the analyses of molecular (memetic) variance. The parameters estimating migrational and mutational inputs support these findings by showing that the populations are rather isolated, with mutation rates higher than meme flow. Nonetheless there is an association between memetic and geographical distances, which indicate that neighbouring populations share more memes than distant populations. We know that populations of different morphology mix during winter (Prŷs-Jones, 1984; Amato et al., 1994). If young reed bunting males keep acquiring songs and song elements through their first winter and up to the beginning of the first reproductive season, as in indigo buntings (*Passerina cyanea*; Payne, 1982), white-crowned sparrows (*Zonotrichia leucophrys*; Baptista and Morton, 1988) and song sparrows (*Melospiza melodia*; Beecher, 1996), they can acquire song elements of early singing adults of the opposite subspecies group, thus effectively mixing meme pools of neighbouring populations, even if they belong to a different subspecies. Geographical distances among breeding sites, also by affecting migration patterns and winter distribution of populations, would be more significant in their cultural differentiation than morphology.

The lack of between subspecies group memetic differences indicates that the groups are not yet culturally differentiated even though they are morphologically, ecologically and, partially, genetically divergent (Isenmann, 1990; Amato et al., 1994; Byers, 1995; Grapputo et al., 1998), in partial agreement with playback experiments (Matessi et al. 2000b). The present results, together with the analysis of variation of quantitative properties of reed bunting song between subspecies groups (Matessi et al. 2000a), seem to indicate that the syllables as such have little meaning for recognition between morphs, while what is relevant is the rule for their combination.

Quantitative analyses show that southern populations have a more complex song structure, each individual using more syllable types in its song sequence, and the pattern of variation correlates better with morphological differences than with geographical distances (Matessi et al., 2000a). A reflection of this that we found in the present memetic analyses is the higher F_{ST} value among southern populations taken separately, which indicates that these are more culturally diverse than northern populations, and the results on multisyllable memes (see below). In an extreme but useful linguistic analogy, it is as if the vocabulary is the same or similar for both morphs and what changes is the syntax. Balaban (1988) obtained similar results with playback experiments on swamp sparrow (*Melospiza georgiana*) song syntax. Both males and females of one population responded differently to playback of two sets of songs differing only in note order, and typical of their own and of a foreign population respectively (Balaban, 1988).

The explanation in our case is that young reed buntings can learn single syllables of either subspecies, but then place them in the temporal and sequence patterns typical of their own, as has been demonstrated for other species (review in Baptista, 1996, but see Podos et al., 1999). The overlap of breeding ranges, resulting in a possible “cultural hybrid” zone (Matessi et al. 2000a) would further increase this effect, especially if philopatry of populations is limited. Similar results, but with a different approach, were recently obtained for song sparrows, where the song type, and not the constituent units of song, is the fundamental unit in the male’s repertoire (Searcy et al., 1999). In the chaffinch populations of New Zealand and Chatham Islands, the two types of variation in song, quantitative and memetic, gave congruent results, possibly because of the low degree of divergence of these populations in ecology and morphology (Baker and Jenkins, 1987). The analysis of memetic differentiation among chaffinch populations on islands and mainland showed a clustering corresponding to island archipelagos, with the mainland populations closer together than island populations (Lynch and Baker, 1994).

The generally high within-population level of variability revealed by multiple-syllable memes is due, partly, to the high variability in number of syllable types per song among individuals and populations (Matessi et al., 2000a), but, more probably, to very high recombination rates of syllables. Syllables in the reed bunting are probably used independently of each other, as is evident when males sing the "mated", or slow, singing style (Ewin, 1976; Nemeth, 1996), associating syllables in a more or less random sequence. The only exceptions seem to be two-syllable memes of southern populations and three-syllable memes in the Spanish population, which also has the lowest one-syllable meme diversity. The southern group of populations also has a higher index of mutational divergence (γ) and a higher F_{ST} value than the northern group. These results could be attributed to bottleneck effects after the recent separation of the populations (Lynch et al., 1989; Burnell, 1998; Grapputo et al., 1998), but the data do not offer a strong support to this hypothesis and interpretations should be cautious.

A noticeable result is the incidence of "point" (i.e. single-syllable shape) mutations of memes compared to meme flow, especially related to results of studies of other species. The levels of meme flow are low relative to those calculated for wood thrush (*Catharus mustelinus*), lazuli bunting (*Passerina amoena*) and tree sparrow (*Passer montanus*), and are comparable only to those among chaffinch populations (Lynch, 1996, p. 194). Meme mutation rates in reed bunting are, on the contrary, similar to those of the mentioned species, and up to four times as high as migration rates. The relationship between movement of memes and movement of individuals is complex and depends on the number of memes carried by a migrating individual and the timing of the migration in relation with the song learning stage of the immigrant and the local residents (Lynch, 1996). There are limits to the extrapolation of such cultural parameters to population demography, but some parallels are possible. Reed buntings are rather selective with regard to breeding habitats, and in western Europe the suitable habitats are fragmented. Therefore, reed bunting populations could have population memetic dynamics similar to island populations, like the chaffinch populations analysed by Lynch (1996). The breeding habitats, furthermore, have a limited capacity, populations are comparatively small and thus drift and mutation of memes would explain the high cultural divergence of the populations.

We point out the good correspondence of the results obtained following the population memetics methods suggested by Lynch (1996), and those obtained by directly applying standard population genetics algorithms to meme frequencies, as implemented in molecular analysis software.

We believe that our results contribute significantly to the knowledge of the little explored aspect of cultural evolution in polymorphic species undergoing complex biological evolutionary processes. We also add to the knowledge of the role of song diversity in population isolation and, possibly, speciation processes. We finally suggest how population genetics models can be further adapted to compare cultural diversity among groups of populations.

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