



## GEOGRAPHIC VARIATION IN SONGS OF THE TREE PIPIT (*ANTHUS TRIVIALIS*) AT TWO SPATIAL SCALES

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**ABSTRACT.**—We studied geographic as well as individual variation of songs in five Czech populations of the Tree Pipit (Motacillidae: *Anthus trivialis*), a passerine bird with a medium-sized syllable repertoire and complex song. We focused on repertoire composition at the level of syllables (the smallest invariant song units) and of structures that are potentially important in recognition among individuals (i.e., bi-syllables, or regular repetitions of two different syllables) and among populations (introductory phrases). We tested the hypotheses that the repertoires reflect local dialects (i.e., different male origins) and that within-site similarities of male repertoires are distance dependent. The populations studied differed significantly in all analyzed characteristics. Male origin explained ~18% of the variation in individual syllable repertoires. However, no clear within-site geographic structure in repertoire similarity was observed, either between closest neighbors or on larger scales. We observed a tendency for increased syllable sharing among males in a small and dense isolated population, which is consistent with recent studies that suggest the existence of strong effects of habitat fragmentation on geographic patterns of song variation. High individual variation was observed in bi-syllable repertoires, but whether this facilitates individual recognition is unknown and in need of further study. Received 13 May 2009, accepted 13 October 2009.

Key words: *Anthus trivialis*, complex song, individual recognition, local dialects, repertoire similarity, Tree Pipit.

### Variation géographique des chants d'*Anthus trivialis* à deux échelles spatiales

**RÉSUMÉ.**—Nous avons étudié les variations géographiques et individuelles des chants parmi cinq populations tchèques d'*Anthus trivialis*, un passereau de la famille des Motacillidés ayant un répertoire de syllabes de la taille moyenne et un chant complexe. Nous avons porté notre attention sur la composition du répertoire au niveau des syllabes (les plus petites unités de chant invariables) et des structures potentiellement importantes dans la reconnaissance entre les individus (bi-syllabes, i.e., répétitions régulières de deux syllabes différentes) et parmi les populations (phrases d'introduction). Nous avons testé les hypothèses que les repertoires reflètent les dialectes locaux (i.e. différentes origines des mâles) et que les similarités des repertoires des mâles dans un site donné dépendent de la distance. Les populations étudiées différaient significativement à travers de toutes les caractéristiques analysées. L'origine des mâles expliquait ~18% de la variation dans les repertoires de syllabes des individus. Toutefois, aucune structure géographique claire de la similarité des repertoires au sein des sites n'a été observée, ni entre les voisins les plus proches ni sur une plus grande échelle. Nous avons observé une tendance à un partage des syllabes parmi les mâles plus marqué dans une petite population isolée et dense, ce qui est cohérent avec les études récentes qui suggèrent l'existence d'effets importants de la fragmentation de l'habitat sur les patrons géographiques de la variation des chants. Une forte variation individuelle a été observée dans les repertoires bi-syllabiques mais il n'est pas clair si cela facilite la reconnaissance entre les individus; une étude plus approfondie est donc nécessaire.

BIRD SONGS REFLECT genetic as well as cultural evolution (Catchpole and Slater 1995), and both methods of information transmission may co-occur. Distinct and fast-evolving variation in song structure within species from different geographic areas is therefore common. Geographic variation in song continues to be studied intensively after several decades of work (reviewed in Podos and Warren 2007) because an understanding of processes that lead to micro- and macro-regional song variation may

elucidate the timing of and social influence on vocal learning, genetic influences on song structure, and other aspects of bird biology, and provide indirect information on dispersal and migration (Mundinger 1982, Lynch 1996, Martens 1996, Slabbekoorn and Smith 2002, Tracy et al. 2009). Geographic song variation may also reflect various ecological influences, such as interspecific competition (Doutrelant and Lambrechts 2001), habitat fragmentation (e.g., Osiejuk et al. 2003, Laiolo and Tella 2007), and

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adaptations of song characteristics to sound transmission properties in local habitats (Wiley 1991, Van Dongen and Mulder 2006). Rapid changes in the latter two are often related to human activities; for example, rapid adaptations in song characteristics have been observed in bird populations that are affected by anthropogenic noise (Slabbekoorn and Peet 2003). Given that important song structures with functions that are subject to differential selection pressures (e.g., mate attraction vs. individual recognition) may show different patterns at various spatial scales, comparing geographic variation in song structures may be an appropriate approach for testing their potential functions.

Although geographic song variation has been analyzed in numerous bird taxa, most studies have focused on species with rather simple songs and small repertoire sizes (1–4 song types per male), such as subspecies of White-crowned Sparrow (*Zonotrichia leucophrys*; reviewed by Mundinger [1982] and more recently studied by, e.g., Nelson [1999]), Ortolan Bunting (*Emberiza hortulana*; Conrads and Conrads 1971, Osiejuk et al. 2003), and Black-capped Chickadee (*Poecile atricapillus*; Ficken et al. 1978, Kroodsma et al. 1999). Analyses of geographic variation in bird species that allegedly have large repertoire sizes are available as well. However, most such species do not have complex songs, but rather their males sing a relatively large number of different simple songs composed of a few elements; good examples are Marsh Wren (*Cistothorus palustris*) and Sedge Wren (*C. platensis*) (Kroodsma and Verner 1978) and Rufous-sided Towhee (*Pipilo erythrophthalmus*; Borror 1975).

The studies listed above share the typical approach used to evaluate geographic song variation: examination of the distribution of whole songs, that is, song types. However, song types are not easily distinguishable in birds with complex songs, in which basic song units can be organized in many ways. Alternative approaches are therefore needed to analyze their repertoires. In his study on Winter Wrens (*Troglodytes troglodytes*), Kroodsma (1980) showed that geographic variation might be detectable when analysis focuses on the distribution of basic units of which songs are composed, such as syllables. Tracy and Baker (1999) also suggested that examining geographic variation and population differences at the syllable level might be important even in species whose song can be analyzed at the level of song type, because song type and syllable use might show different patterns.

However, in spite of Kroodsma's (1980) challenge for more work on geographic variation in the songs of "complex songsters," only a few studies have assessed syllable sharing with the aim of revealing geographic variation in birds with higher song complexity. Examples of such an approach are papers that show differences in syllable use among individual House Finches (*Carpodacus mexicanus*) from the center and edge of the species' distribution area (Pytte 1997), geographic variation in syllable sharing among male Serins (*Serinus serinus*; Mota and Cardoso 2001), and the recent demonstration of microgeographic variation in syllable use in Sky Larks (*Alauda arvensis*; Briefer et al. 2009).

We focused on variation in repertoire compositions of the Tree Pipit (Motacillidae: *Anthus trivialis*), a passerine with an intermediate syllable repertoire size (6–20 different syllable types per individual) that is combined into relatively complex songs (Petrušková et al. 2008; see Fig. 1). In previous detailed work that described the structure and complexity of Tree Pipit songs in the

Czech Republic (Petrušková et al. 2008), we noted high variability in the syllable composition of songs among individual birds, and especially among birds from different localities, at an intermediate geographic scale (35–250 km). In each of the five studied populations, we detected a substantial proportion (one third to two thirds) of unique syllables that were not recorded elsewhere; populations also differed in the dominant syllable types used by individual males in song introductions.

In the present study, we analyzed data on the song composition of 90 male Tree Pipits from these five Czech study sites in more detail to compare the repertoires of males within and among geographically separated populations. To our knowledge, this is the first analysis of geographic song variation in any species of the genus. Together with syllable repertoires, we focused on geographic patterns in the use of specific structures within songs—introductory phrases and the so-called "bi-syllable repeats" (see below; Fig. 1)—that have been proposed to play a role in dialect and individual recognition, respectively (Petrušková et al. 2008). We tested the hypotheses that (1) geographic origin is reflected in high within-site similarity of individual male repertoires (assessed for all three above-mentioned structures: syllables, bi-syllables, and introductory phrases) and that (2) neighboring birds (i.e., with territories <300 m apart) have more similar repertoires (presumably because of copying) than randomly chosen local birds.

## METHODS

*Study species.*—The Tree Pipit is a common and widespread Palearctic songbird. It is a cryptically colored ground-nesting species in which sexual plumage and size dimorphism are absent; however, the singing behavior of males is pronounced. After territory establishment, the core ranges where males sing seem to be stable during the breeding season (Kumstátová et al. 2004). Tree Pipits defend their territory by singing from high posts, usually trees, or in characteristic song flights; consequently, there are two main types of male songs (the common "perched" and less common "flight" songs; Wallschläger 1984, Alström and Mild 2003, Petrušková et al. 2008; Fig. 1A). Flight songs show higher complexity, are longer, and contain a greater number of different syllables than perched songs. However, some consistent patterns, such as the preference of introductory syllable type or the typical position of some syllables or structures, can be found in both song categories (Petrušková et al. 2008).

*Study populations.*—Singing territorial male Tree Pipits were recorded from 2002 through 2005 at five study sites (further labeled by the name of the respective region) in the Czech Republic, covering an elevational gradient from 360 to 1,400 m above sea level. Distances between the study sites ranged from 35 to 250 km (Fig. 2, inset).

The first site (F in Fig. 2; 49.0°N, 13.6°E; 960–1,160 m elevation;  $n = 39$  males) is located in the Bohemian Forest mountain range (name in Czech: Šumava), around the former village Knížecí Pláně, which was abandoned in the 1950s. The second site (U; 50.4°N, 13.8°E; 360–509 m elevation;  $n = 13$  males) lies in the Bohemian Uplands (České středohoří) around two adjacent steep conic volcanic hills, Oblík and Srdov. The third site (O; 50.7°N, 13.7°E; 750–875 m elevation;  $n = 12$  males) is located in the Ore Mountains (Krušné hory) on a plateau around the hill Oldříšský

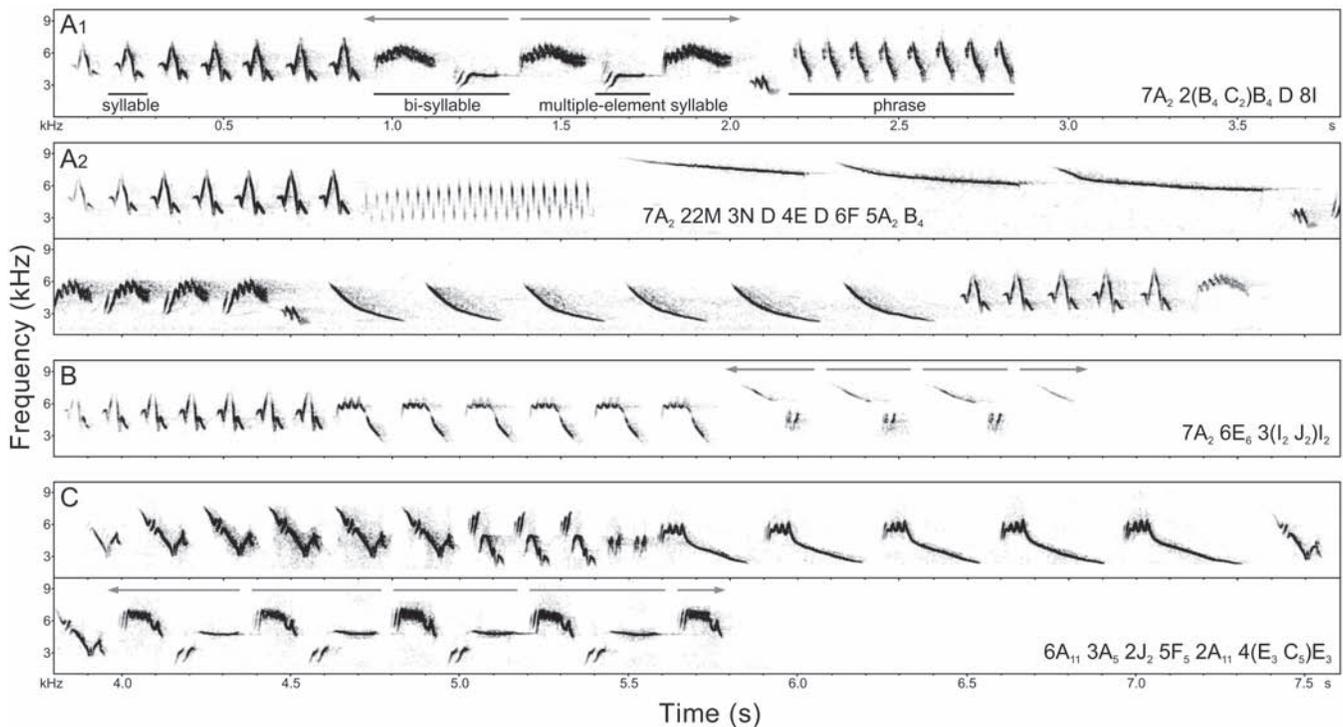


FIG. 1. An example of the spectrograms of Tree Pipit songs, illustrating the features analyzed. (A1) A perched song of a male from the Ore Mountains. (A2) A flight song of the same individual. (B) A perched song of another individual from the same site. (C) A perched song of a male from the Giant Mountains. For each song, the encoded sequence of syllables or bi-syllables is provided: syllable types are indicated by arbitrarily chosen letters with (or without) subscripts, those composing a bi-syllable are enclosed in parentheses, preceding numerals indicate number of repetitions, and phrases are separated by blank spaces. All bi-syllable repeats in the example songs are indicated by gray arrows (interrupted at bi-syllable borders); these often end with an incomplete repeat (an "orphan syllable"). Note that songs of individuals A and B start with a repetition of the same syllable (introductory phrase). Additional spectrogram examples and a more detailed description of song structure and the terminology used are provided in Petrusková et al. (2008).

vrch near Moldava. The fourth site (L; 50.9°N, 14.5°E; 450–470 m elevation;  $n = 11$  males) lies at the edge of the Lusatian Mountains (Lužické hory), close to the village Rybníště. The fifth site (G; 50.7°N, 15.6°E; 1,090–1,350 m elevation;  $n = 15$  males) is on the slopes of the Giant Mountains (Krkonoše). More details about the studied populations and sites (e.g., population density and habitat types) are provided by Petrusková et al. (2008).

*Song recording and analysis.*—Birds were recorded between 0600 and 1800 hours CET on a Marantz PMD 222 analogue tape recorder with a Sennheiser shotgun microphone (Sennheiser K6 powering module with a ME 67 microphone head). All territorial males were recorded only once (mostly in a single session), and the location of their territories was marked on a map or aerial photograph of the study site. This ensured unequivocal identification of individual males. The time of day and behavior of the subject were noted during each recording. The analogue recordings were digitized using a personal computer equipped with the sound card Sound Blaster Audigy 2 Platinum, with a 44.1 kHz/16 bit sampling rate. Further analyses were performed in Avisoft SASLab Pro, version 4.3x (Specht 2007). The analyzed material consisted of 2,166 songs recorded from 90 males at the five study sites (Petrusková et al. 2008).

The approach used for the basic analyses of Tree Pipit songs is described in detail by Petrusková et al. (2008). Although the recorded Tree Pipit songs varied substantially in duration (range: 0.6–15.8 s, average  $\pm$  SD =  $3.3 \pm 2.1$  s), individual songs were separated by distinct gaps and could be easily identified. Spectrograms of several songs, together with the terminology used, are provided in Figure 1. The structure of each song was described as a sequence of syllables (the minimal units of song production, defined as the smallest invariant units in a male's repertoire). Each syllable was usually composed of a single element (uninterrupted trace in the spectrogram), but multiple-element syllables also occasionally occurred (elements in such syllables were always observed together). Syllables were often repeated several times (together forming a phrase). The common presence of "bi-syllables," distinct combinations of two different syllable types (which may also occur separately), is characteristic of Tree Pipit songs (Petrusková et al. 2008). Like individual syllables, bi-syllables are usually combined in repeats (phrases) that sometimes end with an incomplete bi-syllable (see Fig. 1). Because of the frequent repetitions of bi-syllables in songs, we considered them equivalent to individual syllables during computations of various structural parameters, such as phrase versatility (Petrusková et al. 2008).

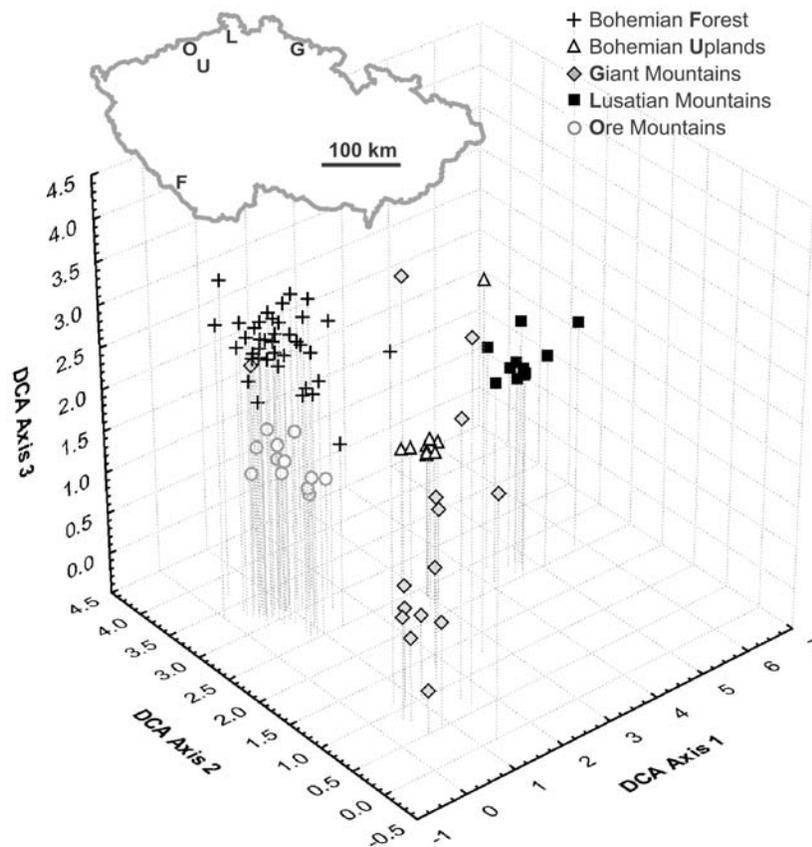


FIG. 2. Detrended correspondence analysis (DCA) of syllable repertoires of male Tree Pipits, based on presence–absence of syllable types. Each symbol represents a single male. The three DCA axes cover 13.5% of variation. Outline of the Czech Republic in the inset shows the position of the study sites (indicated by bold letters in the legend); a more detailed map is given in Petrusková et al. (2008).

The syllables detected were assigned to a particular syllable type in a two-stage procedure, each done by a different person to ensure reproducibility. T.P. annotated all recorded songs by visually inspecting the spectrograms. A template spectrogram was then saved for each presumably different syllable type. This initial categorization of syllables was subsequently verified by T.S.O., with a spectrogram cross-correlation algorithm using the Avisoft SASLab “Scan for template spectrogram patterns” function (settings are provided in Petrusková et al. 2008). A template of each putatively different syllable type was used to classify relevant syllables within all analyzed songs, and the results of the classification of visually similar but presumably different syllable types were compared. In cases in which automated classifications of such similar syllable types by two or more different templates overlapped between the recordings (i.e., they could not be reliably differentiated), these were pooled together and considered a single syllable type.

The syllable sequence in each song was encoded with a symbolic notation (see examples in Fig. 1), which allowed subsequent calculation of the syllable and bi-syllable repertoires of individual males (expressed as presence–absence of the respective units), as well as the identification of syllables in particular song positions. This approach is described in detail by Petrusková et al. (2008). For each male, we also calculated the repertoire of syllable or bi-syllable repeats used as openings of the songs (see Fig. 1), the

so-called “introductory phrases,” because these are apparently more often shared among males from the same population (Petrusková et al. 2008).

*Statistical analyses.*—To visualize the intra- and inter-population variation of syllable repertoires, we used a detrended correspondence analysis (DCA) based on the presence–absence of each syllable type in the songs of each recorded male. A canonical correspondence analysis (CCA) was used to quantify the proportion of repertoire variation that could be explained by male origin (study site). The significance of the relationship between site and repertoire composition was then tested by a Monte Carlo test with 1,000 permutations. These analyses were performed in CANOCO for Windows, version 4.5 (ter Braak and Šmilauer 2002).

Data on individual male repertoires were used to construct three similarity matrices using the Jaccard similarity coefficient ( $J$ ), which covered the similarity of syllable repertoires, introductory phrase repertoires, and bi-syllable repertoires between males. The Jaccard coefficient is calculated as  $J = M_{11} / (M_{01} + M_{10} + M_{11})$ , where  $M_{11}$  represents the total number of elements of the respective type shared between a given pair of males and  $M_{01}$  and  $M_{10}$  are sums of element types unique to each of the respective males. The coefficient values may range from 0 to 1, with 0 indicating that the repertoires of compared males do not contain any shared elements and 1 indicating that all elements are shared between the

two males. Additionally, we calculated the corresponding matrix of geographic distances (km) between the centers of male territories.

To test our hypotheses in more detail, we conducted three self-designed randomization tests. First, we tested that pairs of males recorded from the same populations in the same year have more similar repertoires than those from different populations. For all five populations, we summed averages of pairwise repertoire similarity calculated separately for each population, and we compared the result with values obtained the same way from 2,000 sets in which the origin of males was randomly reshuffled. Second, we used the same algorithm to compare each pair of populations separately, to test whether the pattern resulting from the first test was consistent. Third, we tested whether close neighbors (i.e., with centers of territories <300 m apart) within each population tended to have more similar repertoires than randomly selected pairs of local males. We calculated the average repertoire similarity of all close-neighbor male pairs recorded at a particular site in the same year and compared it with values obtained in the same way from 2,000 sets in which distances between pairs of males within the site were randomly reshuffled. We also evaluated whether averaging affected the results by using corresponding median values of repertoire similarity instead of averages. The randomization tests were calculated for the similarity matrices of syllables, bi-syllables, and introductory phrases. The resulting *P* values were corrected for multiple tests by Bonferroni correction.

Additionally, we used the Mantel test available in the software ZT (Bonnet and Van de Peer 2002) to check whether there was a significant relationship between the geographic distance of pairs of males, and their repertoire similarity; this was tested on the respective matrices of (1) distances between male territories and (2) repertoire similarities. In contrast to the randomization described above, which specifically tested the hypothesis that neighbors have more similar repertoires than non-neighbors, the Mantel test analyzed whether song similarity has a distance-dependent trend across each study site in its entirety. Given that preliminary observations (Petrusková et al. 2008) as well as results of previous analyses have shown substantial differences in repertoires among sites, we ran the tests solely within sites to focus on intrapopulation spatial variation in repertoire similarity. For each population, the test (using 1,000 random matrix reorderings) was conducted only for the year with the largest number of recorded males. The significance of the results was also corrected for multiple tests.

## RESULTS

*Geographic variation in syllable and bi-syllable repertoires.*—Of 153 different syllable types, 114 (74.5%) were unique to a single study site; the unique syllables formed 34–63% of local repertoires (Table 1). Only 12 syllable types were shared among more than two studied populations, and only 4 of these were recorded in all populations (for more details, see Petrusková et al. 2008). An even stronger tendency for local differentiation was observed in bi-syllable repertoires: >90% of the 64 observed bi-syllable types were locally unique (Table 1), 4 bi-syllable types were shared between two populations (usually the Ore Mountains and Bohemian Forest), and a single type was shared among three populations (Giant Mountains, Ore Mountains, and Bohemian Uplands).

TABLE 1. Numbers of syllable and bi-syllable types detected at study sites, and the number and proportion of syllables and bi-syllables that are unique to each population (in parentheses). The total number of different (bi-) syllable types is lower than the sum of local repertoires because of the presence of (bi-) syllables shared among sites; the sum and proportion of types that are unique to any single population are provided in parentheses in the last row.

Study site	Syllable types	Bi-syllable types
Bohemian Forest	60 (35; 58%)	22 (19; 86%)
Bohemian Uplands	31 (13; 42%)	15 (12; 80%)
Giant Mountains	57 (34; 60%)	16 (14; 88%)
Lusatian Mountains	32 (20; 63%)	7 (6; 86%)
Ore Mountains	35 (12; 34%)	11 (7; 63%)
Total number of types	153 (114; 75%)	64 (58; 91%)

Syllable repertoires of individual males showed a clear geographic structure. Despite high individual variation, most birds from one site had a tendency to cluster together in the detrended correspondence analysis (Fig. 2), which confirms the existence of local dialects in Tree Pipit songs. Differences in the scatter within such clusters nevertheless show that syllable sharing among birds recorded in different regions varies (e.g., compare the high similarity of repertoires in most birds from the Bohemian Uplands and the much more scattered points that represent those from the Giant Mountains). Occasional outliers indicate that birds that use a substantial proportion of unusual, often unique, syllables may also occur even within a population with otherwise homogeneous repertoires (e.g., Bohemian Uplands). Despite the within-site differences, 17.7% of the syllable repertoire variation among males was attributable to geographic origin, and this relationship was highly significant (canonical correspondence analysis,  $P < 0.001$ ).

*Local dialects and individual variation in repertoires.*—The patterns of similarity in the repertoires of neighboring (<300 m apart), local but non-neighboring (>300 m), and distant males (originating from different sites) are summarized for each study site separately in Figure 3. The similarity of male repertoires in all three measures of song composition (presence of syllables, bi-syllables, and introductory phrases) was always higher within than among sites. Randomization tests confirmed that these patterns are highly significant ( $P < 0.001$  for all three tests that compared patterns across all sites). Pairwise comparisons showed significantly higher within-site repertoire similarity in all but 1 of 30 tests (all  $P < 0.01$ , usually an order of magnitude lower, except for the comparison of introductory phrase repertoires between the Lusatian Mountains and Bohemian Forest, with  $P = 0.063$ ).

By contrast, we did not observe any consistent spatial pattern of song differentiation within sites. In most analyses, the randomization test did not show any tendency for neighboring birds to have more similar repertoires than other local birds, which is in agreement with the inconsistent patterns in Figure 3 (boxplots N and L). The single exception was the Bohemian Forest, where this tendency was observed for syllable repertoires ( $P < 0.0015$ ; result significant after Bonferroni correction for multiple tests). However, it was not observed in tests that compared median instead of the mean similarity indices; in such cases, no comparison showed increased similarity for close neighbors. In concordance

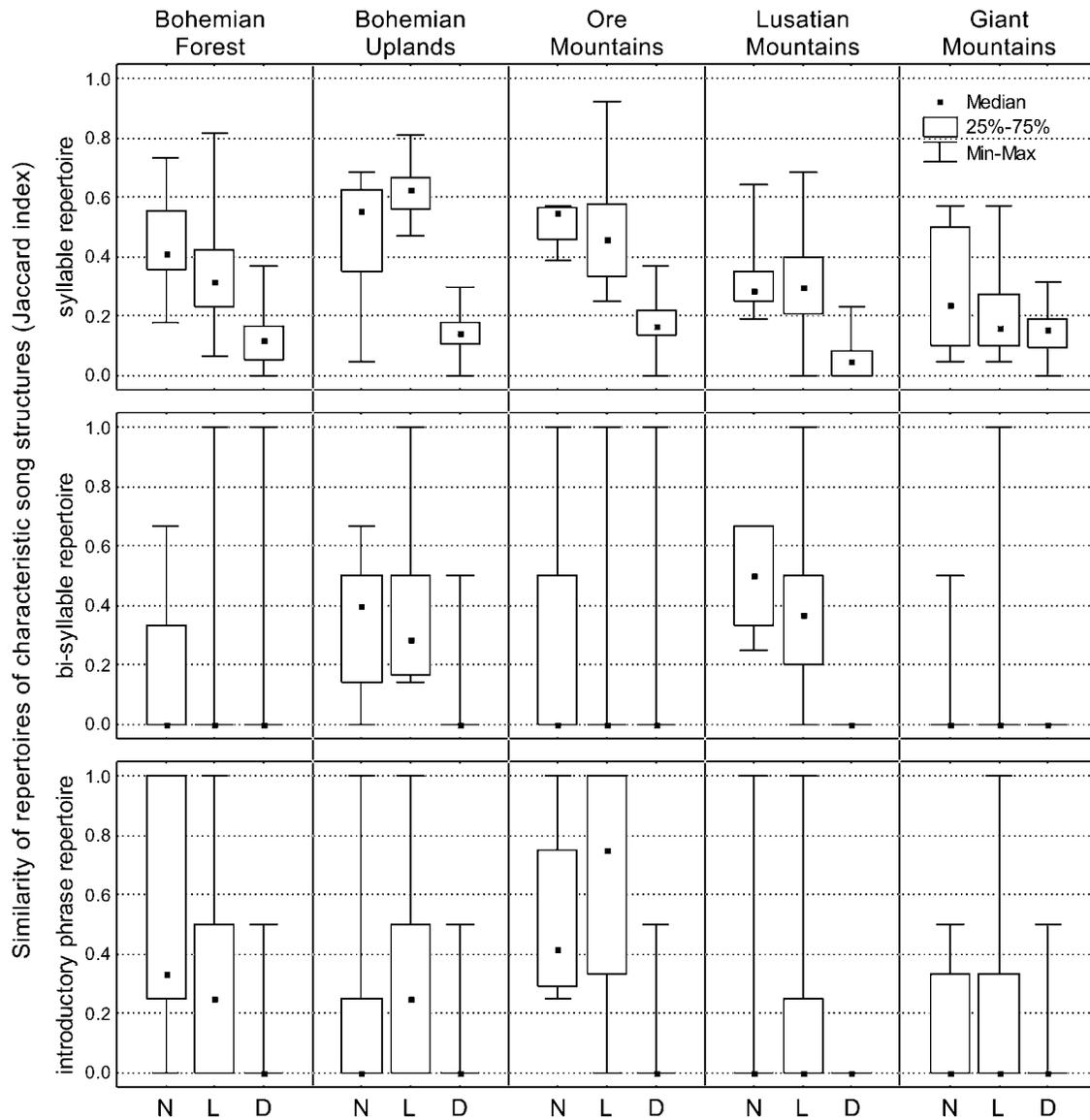


FIG. 3. Similarity of repertoires of song structures (Jaccard index) of male Tree Pipits from all study sites, calculated for all syllables, bi-syllables, and introductory phrases. Boxplots summarize pairwise comparisons of all close neighbors within the site (*N*; distance < 300 m), all local non-neighbor males (*L*; distance > 300 m), and comparisons with all males from other, distant sites (*D*; distance > 35 km). Within-site comparisons are calculated only for males recorded in the same year.

with these results, none of the Mantel tests suggested an increased similarity of song with increased territory proximity after we applied corrections for multiple tests.

The pattern of bi-syllable sharing among males was particularly interesting. As has been shown before (Petrušková et al. 2008), individual bi-syllable repertoires were usually very small (<2 bi-syllable types per male, on average, in contrast to an average syllable repertoire of >11 types), and more than half of the bi-syllables recorded in our study were used solely by a single male. Bi-syllable sharing occurred (Fig. 3), but there seemed to be a tendency to avoid the complete sharing of bi-syllable repertoires by males within hearing distance. Only 2 males (in the Ore Mountains) out of the 41 close-neighbor pairs that we compared shared

a single bi-syllable type and did not differ in their bi-syllable repertoire. The remaining males in close proximity differed in at least one bi-syllable type.

#### DISCUSSION

This evidence of clear geographic variation in Tree Pipit songs adds to the few studies that have examined dialects in birds with complicated song structures (Kroodsma 1980, Pytte 1997, Tracy and Baker 1999, Mota and Cardoso 2001, Tracy et al. 2009). The regional influence was apparent in syllable composition as well as in the song components previously suggested as potentially important in individual (bi-syllable) or population (introductory phrase)

recognition (Petrušková et al. 2008). What factors may be critical in the formation of such pronounced geographic variation?

Two broad scenarios have been proposed to explain the main processes that influence individual repertoire compositions (Krebs 1977). The first stresses the role of females, which evaluate repertoires as an important criterion in choosing their mates; in such cases, repertoires are driven by sexual selection (e.g., Lampe and Saetre 1995, Mountjoy and Lemon 1996, Reid et al. 2004). Females may contribute to dialect maintenance by preferentially mating with males that sing a local dialect (e.g., O’Loughlen and Rothstein 2003), but opposite tendencies have also been found (e.g., McGregor and Thompson 1988). The second scenario proposes that male–male interactions are more important in repertoire formation. Maintenance of a local dialect may certainly be enhanced by song learning from adults in the neighborhood; young males may even match their own songs to those of immediate neighbors (Nordby et al. 1999, Nicholson et al. 2007). In some species, song or repertoire sharing with neighbors correlates with successful territory tenure within a season (Beecher et al. 2000) as well as in the long term (Grieffmann and Naguib 2002).

Although we cannot exclude the possibility that female mate choice influences repertoire formation in Tree Pipits, we presume that song learning from local males and subsequent interactions with neighbors are more important for male repertoires. This species shows high fidelity to natal area. Available studies showed that 51–79% of ringed males and 32–50% of ringed females returned to their breeding place (van Hecke 1981, Meury 1989). Returning adult males settled in territories that were, on average, ~200 m from those occupied in the previous year; dispersal of yearlings was only ~1,600 m from their natal site (Meury 1989).

We assume that the syllable richness and compositional stability of local repertoires may depend on local density and the ability of males to disperse. This might be demonstrated by populations that show contrasting patterns in our data set (Fig. 2), for instance, (1) the Bohemian Uplands and (2) the Giant Mountains and Bohemian Forest. The former is an isolated locality surrounded by habitats unsuitable for Tree Pipits; the species has been in decline there since at least the end of the 1990s (T. Petrušková unpubl. data), presumably owing to the loss of suitable patches because of the growth of bushy vegetation. During the years when recordings were obtained, the local population (~13 singing males) occupied essentially all suitable territories, which resulted in relatively high population densities (Petrušková et al. 2008). Most males, when settled, could hear several other individuals nearby. Together with high nest-site fidelity, this seemed to result in a generally high similarity among syllable repertoires (Figs. 2 and 3) within the population, in which only a single male, apparently a newcomer, used mostly syllables unshared by any other local bird.

On the other hand, the repertoires of males in other areas show more scatter (Fig. 2). In the Giant Mountains and Bohemian Forest, in particular, this corresponds with the distribution of recorded birds. Many of them occupied territories that were isolated by surrounding forest (Petrušková et al. 2008), and communication and interaction among local males was probably more limited than in the Bohemian Uplands. Additionally, no other study population was as isolated, so exchange of males with surrounding areas and chances for birds to disperse were likely higher. This probably resulted in richer site-specific repertoires but also higher dissimilarity among local males.

The patterns described above have also been observed in Dupont’s Lark (*Chersophilus duponti*): males from populations isolated by fragmented habitats showed significantly higher sharing of song repertoires than birds from populations in more continuous habitat (e.g., Laiolo and Tella 2007, Laiolo et al. 2008). Recently, Briefer et al. (2010) obtained similar results for the Sky Lark. They showed that neighboring birds in fragmented habitats shared more syllables and sequences of syllables than males in undisturbed areas. They also showed that Sky Lark songs contain a syllable sequence typical of all males from a particular site, which was used to discriminate between neighbors and strangers (Briefer et al. 2008a).

The tendency of Tree Pipits to use only a few introductory phrases, some of which are typical of local repertoires and may also serve as local signatures, has already been shown (Petrušková et al. 2008). This is in contrast with the use of bi-syllable types, which showed very high individual variability and was proposed as an important cue for individual recognition. Our casual observations suggest that males might tend to alter bi-syllable use toward unshared bi-syllables in reaction to neighbors. When some bi-syllables were shared between neighboring males, the neighbors tended to use nonshared types: among 13 pairs of neighbors in which some bi-syllable sharing occurred, only 3 used the shared bi-syllable type more often. However, a focused study would be needed to assess the consistency of this pattern. The hypothesized function of bi-syllable repertoires as individual signatures could be tested by playbacks that examine neighbor–stranger recognition by using artificially altered stimuli, in which bi-syllables used by known birds are replaced with others.

Despite substantial evidence that birds can recognize the songs of individual males, both in intrasexual (especially neighbor–stranger; e.g., Brooks and Falls 1975, Molles and Vehrencamp 2001, Skierczyński et al. 2007, Briefer et al. 2008b) and intersexual (e.g., Beguin et al. 1998, Lampe and Slagsvold 1998, Blumenrath et al. 2007) interactions, the cues that enable such recognition are rarely discussed. This may be attributable to the assumption that birds evaluate many song features simultaneously and that such a process cannot be reduced to specific structures only. However, particular features have been suggested as useful for individual recognition in certain species: song-type variants as well as repertoire composition in Banded Wrens (*Thryothorus pleurostictus*; Molles and Vehrencamp 2001), individual signatures based on specific syllable sequences in Canaries (*Serinus canaria*; Lehongre et al. 2008), specific introductory syllables in Great Reed Warblers (*Acrocephalus arundinaceus*; Węgrzyn et al. 2009), and syntactical arrangement of syllables in Sky Larks (Briefer et al. 2009). Naguib and Todt (1998) suggested several possibilities for the coding of individuality in songs of a highly complex singer, the Thrush Nightingale (*Luscinia luscinia*).

Two studies have discussed possible cues that may encode individual identity in the songs of pipit species. Osiejuk et al. (2007) found individual differences in frequency parameters and fine note structure in the Tawny Pipit (*Anthus campestris*) and suggested that individuality may be encoded in whole songs. However, the songs of this species are very simple (Wallschläger 1984); other pipit species may therefore use different cues. Elfström (1990) tested interspecific recognition between two species that sing longer and more complex songs that are similar to each other, the Meadow Pipit (*A. pratensis*) and Rock Pipit (*A. petrosus*), and suggested that the first, highly variable part of the song contains

cues for individual recognition; his experiments nevertheless did not reveal structures that are crucial for this process.

Although we observed clear geographic differences among Tree Pipit populations, a large part of any bird's repertoire could not be considered locally specific. This, together with the site fidelity of Tree Pipits, suggests that improvisation increases the individuality of repertoires and could be an important component of vocal development in this species, which is unlikely the case for pipits with more simple songs, such as the Tawny Pipit (Osiejuk et al. 2007).

The complex song of the Tree Pipit, with its characteristically differentiated structures that likely have different functions in species communication, seems a good model for studying spatial variation of acoustic signals that evolved under different selection pressures (species recognition, neighbor recognition, sexual selection, etc.). Such a model may be particularly promising, because there are species within the genus *Anthus* that differ substantially in song complexity, repertoire size, and sharing pattern of song structures, despite their close phylogenetic relationship (Wallschläger 1984, Voelker 1999). In the future, this may allow greater in-depth research on the patterns of geographic song variation from an evolutionary perspective.

#### ACKNOWLEDGMENTS

R. S. Fuchs provided the recording equipment, P. Linhart recorded all pipits in the Lusatian Mountains and some in the Bohemian Forest, and V. Pavel and B. Chutný helped substantially during the field work in the Giant Mountains. The study was funded by the Czech Ministry of Education (projects FRVŠ 2820/2003 and MSM0021620828). The Czech and Slovak Ethological Society and the Mobility Fund of Charles University supported a study visit for T.P. in the Department of Behavioural Ecology, Adam Mickiewicz University, Poznań. We thank J. Flegr for valuable advice on randomization tests, D. Hardekopf for language revisions, and Alfred M. Dufty, Jr., and three anonymous reviewers for helpful comments that substantially improved the manuscript.

#### LITERATURE CITED

- ALSTRÖM, P., AND K. MILD. 2003. Pipits and Wagtails of Europe, Asia and North America. Christopher Helm, London.
- BEECHER, M. D., S. E. CAMPBELL, AND J. C. NORDBY. 2000. Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. *Animal Behaviour* 59:29–37.
- BEGUIN, N., G. LÉBOUCHER, AND M. KREUTZER. 1998. Sexual preferences for mate song in female Canaries (*Serinus canaria*). *Behaviour* 135:1185–1196.
- BLUMENRATH, S. H., T. DABELSTEEN, AND S. B. PEDERSEN. 2007. Vocal neighbour–mate discrimination in female Great Tits despite high song similarity. *Animal Behaviour* 73:789–796.
- BONNET, E., AND Y. VAN DE PEER. 2002. ZT: A software tool for simple and partial Mantel tests. *Journal of Statistical Software* 7(10):1–12.
- BORROR, D. J. 1975. Songs of the Rufous-sided Towhee. *Condor* 77:183–195.
- BRIEFER, E., T. AUBIN, K. LEHONGRE, AND F. RYBAK. 2008a. How to identify dear enemies: The group signature in the complex song of the skylark *Alauda arvensis*. *Journal of Experimental Biology* 211:317–326.
- BRIEFER, E., T. AUBIN, AND F. RYBAK. 2009. Response to displaced neighbours in a territorial songbird with a large repertoire. *Naturwissenschaften* 96:1067–1077.
- BRIEFER, E., T. S. OSIEJUK, F. RYBAK, AND T. AUBIN. 2010. Are bird song complexity and song sharing shaped by habitat structure? An information theory and statistical approach. *Journal of Theoretical Biology* 262:151–164.
- BRIEFER, E., F. RYBAK, AND T. AUBIN. 2008b. When to be a dear enemy: Flexible acoustic relationships of neighbouring skylarks, *Alauda arvensis*. *Animal Behaviour* 76:1319–1325.
- BROOKS, R. J., AND J. B. FALLS. 1975. Individual recognition by song in White-throated Sparrows. I. Discrimination of songs of neighbors and strangers. *Canadian Journal of Zoology* 53:879–888.
- CATCHPOLE, C. K., AND P. J. B. SLATER. 1995. Bird Song: Biological Themes and Variations. Cambridge University Press, Cambridge, United Kingdom.
- CONRADS, K., AND W. CONRADS. 1971. Regionaldialekte des Ortolans (*Emberiza hortulana*) in Deutschland. [Regional dialects of Ortolan Bunting (*Emberiza hortulana*) in Germany.] *Vogelwelt* 92:81–100. [In German.]
- DOUTRELANT, C., AND M. M. LAMBRECHTS. 2001. Macrogeographic variation in song—A test of competition and habitat effects in Blue Tits. *Ethology* 107:533–544.
- ELFSTRÖM, S. T. 1990. Individual and species-specific song patterns of Rock and Meadow pipits: Physical characteristics and experiments. *Bioacoustics* 2:277–301.
- FICKEN, M. S., R. W. FICKEN, AND S. R. WITKIN. 1978. Vocal repertoire of Black-capped Chickadee. *Auk* 95:34–48.
- GRIEBMANN, B., AND M. NAGUIB. 2002. Song sharing in neighboring and non-neighboring Thrush Nightingales (*Luscinia luscinia*) and its implications for communication. *Ethology* 108:377–387.
- KREBS, J. R. 1977. The significance of song repertoires: The Beau Geste hypothesis. *Animal Behaviour* 25:475–478.
- KROODSMA, D. E. 1980. Winter Wren singing behavior: A pinnacle of song complexity. *Condor* 82:357–365.
- KROODSMA, D. E., B. E. BYERS, S. L. HALKIN, C. HILL, D. MINIS, J. R. BOLSINGER, J.-A. DAWSON, E. DONELAN, J. FARRINGTON, F. B. GILL, AND OTHERS. 1999. Geographic variation in Black-capped Chickadee songs and singing behavior. *Auk* 116:387–402.
- KROODSMA, D. E., AND J. VERNER. 1978. Complex singing behaviors among *Cistothorus* wrens. *Auk* 95:703–716.
- KUMSTÁTOVÁ, T., T. BRINKE, S. TOMKOVÁ, R. FUCHS, AND A. PETRUSEK. 2004. Habitat preferences of Tree Pipit (*Anthus trivialis*) and Meadow Pipit (*A. pratensis*) at sympatric and allopatric localities. *Journal of Ornithology* 145:334–342.
- LAILOLO, P., AND J. L. TELLA. 2007. Erosion of animal cultures in fragmented landscapes. *Frontiers in Ecology and the Environment* 5:68–72.
- LAILOLO, P., M. VÖGELI, D. SERRANO, AND J. L. TELLA. 2008. Song diversity predicts the viability of fragmented bird populations. *PLoS ONE* 3:e1822.
- LAMPE, H. M., AND G. P. SAETRE. 1995. Female Pied Flycatchers prefer males with larger song repertoires. *Proceedings of the Royal Society of London, Series B* 262:163–167.
- LAMPE, H. M., AND T. SLAGSVOLD. 1998. Female Pied Flycatchers respond differently to songs of mates, neighbours and strangers. *Behaviour* 135:269–285.

- LEHONGRE, K., T. AUBIN, S. ROBIN, AND C. DEL NEGRO. 2008. Individual signature in canary songs: Contribution of multiple levels of song structure. *Ethology* 114:425–435.
- LYNCH, A. 1996. The population memetics of birdsong. Pages 181–197 in *Ecology and Evolution of Acoustic Communication in Birds* (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.
- MARTENS, J. 1996. Vocalizations and speciation of Palearctic birds. Pages 221–240 in *Ecology and Evolution of Acoustic Communication in Birds* (D. E. Kroodsma and E. H. Miller, Eds.). Cornell University Press, Ithaca, New York.
- MCGREGOR, P. K., AND D. B. A. THOMPSON. 1988. Constancy and change in local dialects of the Corn Bunting. *Ornis Scandinavica* 19:153–159.
- MEURY, R. 1989. Brutbiologie und Ortstreue einer Baumpieperpopulation *Anthus trivialis* in einem inselartig verteilten Habitat des schweizerischen Mittellandes. [Breeding biology and site fidelity in the Tree Pipit *Anthus trivialis* in a landscape with a patchy habitat distribution in the Swiss Lowlands.] *Ornithologische Beobachter* 86:219–233. [In German with English summary.]
- MOLLES, L. E., AND S. L. VEHRENCAMP. 2001. Neighbour recognition by resident males in the Banded Wren, *Thryothorus pleurostictus*, a tropical songbird with high song type sharing. *Animal Behaviour* 61:119–127.
- MOTA, P. G., AND G. C. CARDOSO. 2001. Song organisation and patterns of variation in the serin (*Serinus serinus*). *Acta Ethologica* 3:141–150.
- MOUNTJOY, D. J., AND R. E. LEMON. 1996. Female choice for complex song in the European starling: A field experiment. *Behavioral Ecology and Sociobiology* 38:65–71.
- MUNDINGER, P. C. 1982. Microgeographic and macrogeographic variation in acquired vocalizations in birds. Pages 147–208 in *Acoustic Communication in Birds*, vol. 2 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, New York.
- NAGUIB, M., AND D. TODT. 1998. Recognition of neighbors' song in a species with large and complex song repertoires: Thrush Nightingale. *Journal of Avian Biology* 29:155–160.
- NELSON, D. A. 1999. Ecological influences on vocal development in the White-crowned Sparrow. *Animal Behaviour* 58:21–36.
- NICHOLSON, S. K., K. L. BUCHANAN, R. C. MARSHALL, AND C. K. CATCHPOLE. 2007. Song sharing and repertoire size in the Sedge Warbler, *Acrocephalus schoenobaenus*: Changes within and between years. *Animal Behaviour* 74:1585–1592.
- NORDBY, J. C., S. E. CAMPBELL, AND M. D. BEECHER. 1999. Ecological correlates of song learning in Song Sparrows. *Behavioral Ecology* 10:287–297.
- O'LOGHLEN, A. L., AND S. I. ROTHSTEIN. 2003. Female preference for the songs of older males and the maintenance of dialects in Brown-headed Cowbirds (*Molothrus ater*). *Behavioral Ecology and Sociobiology* 53:102–109.
- OSIEJUK, T. S., J. GRZYBEK, AND P. TRYJANOWSKI. 2007. Song structure and repertoire sharing in the Tawny Pipit *Anthus campestris* in Poland. *Acta Ornithologica* 42:157–165.
- OSIEJUK, T. S., K. RATYNSKA, J. P. CYGAN, AND S. DALE. 2003. Song structure and repertoire variation in Ortolan Bunting (*Emberiza hortulana* L.) from isolated Norwegian population. *Annales Zoologici Fennici* 40:3–16.
- PETRUSKOVÁ, T., T. S. OSIEJUK, P. LINHART, AND A. PETRUSEK. 2008. Structure and complexity of perched and flight songs of the Tree Pipit (*Anthus trivialis*). *Annales Zoologici Fennici* 45:135–148.
- PODOS, J., AND P. S. WARREN. 2007. The evolution of geographic variation in bird songs. *Advances in the Study of Behavior* 37:403–458.
- PYTTE, C. L. 1997. Song organization of House Finches at the edge of an expanding range. *Condor* 99:942–954.
- REID, J. M., P. ARCESE, A. L. E. V. CASSIDY, S. M. HIEBERT, J. N. M. SMITH, P. K. STODDARD, A. B. MARR, AND L. F. KELLER. 2004. Song repertoire size predicts initial mating success in male Song Sparrows, *Melospiza melodia*. *Animal Behaviour* 68:1055–1063.
- SKIERCZYŃSKI, M., K. M. CZARNECKA, AND T. S. OSIEJUK. 2007. Neighbour–stranger song discrimination in territorial Ortolan Bunting *Emberiza hortulana* males. *Journal of Avian Biology* 38:415–420.
- SLABBEKOORN, H., AND M. PEET. 2003. Birds sing at a higher pitch in urban noise—Great Tits hit the high notes to ensure that their mating calls are heard above the city's din. *Nature* 424:267.
- SLABBEKOORN, H., AND T. B. SMITH. 2002. Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society of London, Series B* 357:493–503.
- SPECHT, R. 2007. Avisoft-SASLab Pro, version 4.39. Sound Analysis and Synthesis Laboratory. [Software.] Avisoft Bioacoustics, Berlin.
- TER BRAAK, C. J. F., AND P. ŠMILAUER. 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination, version 4.5. Microcomputer Power, Ithaca, New York.
- TRACY, T. T., AND M. C. BAKER. 1999. Geographic variation in syllables of House Finch songs. *Auk* 116:666–676.
- TRACY, T. T., H. J. ZASADNY, J. G. ERICKSON, AND J. L. SIEMERS. 2009. Syllable and song sharing in a recently established population of House Finches (*Carpodacus mexicanus*). *Auk* 126:823–830.
- VAN DONGEN, W. F. T., AND R. A. MULDER. 2006. Habitat density, song structure and dialects in the Madagascar Paradise Flycatcher *Terpsiphone mutata*. *Journal of Avian Biology* 37:349–356.
- VAN HECKE, P. 1981. Ortstreue, Altersaufbau und Mortalität einer Population des Baumpiepers (*Anthus t. trivialis*). [Site-tenacity, age structure and mortality in a population of the Tree Pipit (*Anthus trivialis*) in northern Belgium.] *Journal für Ornithologie* 122:23–35. [In German with English summary.]
- VOELKER, G. 1999. Molecular evolutionary relationships in the avian genus *Anthus* (Pipits: Motacillidae). *Molecular Phylogenetics and Evolution* 11:84–94.
- WALLSCHLÄGER, D. 1984. Ein bioakustischer Beitrag zur Systematik paläarktischer Motacillidae II. Gesänge und Rufe der Gattung *Anthus*. [A bioacoustical contribution to the systematics of the Palearctic Motacillidae. II. Songs and call-notes of the genus *Anthus*.] *Mitteilungen aus dem Zoologischen Museum in Berlin* 60:37–56. [In German with English summary.]
- WĘGRZYŃ, E., K. LENIOWSKI, AND T. S. OSIEJUK. 2009. Introduce yourself at the beginning—Possible identification function of the initial part of the song in the Great Reed Warbler *Acrocephalus arundinaceus*. *Ornis Fennica* 86:61–70.
- WILEY, R. H. 1991. Associations of song properties with habitats for territorial oscine birds of Eastern North America. *American Naturalist* 138:973–993.