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Structure and complexity of perched and flight songs of the tree pipit (*Anthus trivialis*)

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We analysed 2166 songs of 90 males of the tree pipit (*Anthus trivialis*; Passeriformes: Motacillidae) from five Czech localities to evaluate variation in song characteristics, the song structure and syntax rules, and differences between songs performed in flight and from perches. We measured temporal and spectral song characteristics; structure analysis was based on the identification of individual syllable units. There was a high among-population variation in the repertoire, suggesting substantial differences in local dialects. Flight and perched songs significantly differed in most analysed quantitative characteristics. While both types of songs are apparently used in territorial defence, trill elements within flight songs may also indicate male quality to potential mates. Characteristic bi-syllable repeats within songs were often unique for individual males and may function in individual recognition. Features of tree pipit songs make it a good species for studying song variation and function in birds with complex repertoires.

Introduction

A bird song is one of the most interesting sexually selected traits. Firstly, it is the subject of both intra- and intersexual selection (Catchpole & Slater 1995). Secondly, in many bird taxa including Oscines, aptly named “songbirds”, song is culturally transmitted through learning. The learning patterns, however, vary remarkably among various species (Brenowitz & Beecher 2005). Thirdly, song is a multiple signal: its different parameters, such as rate, frequency, repertoire size and contents, or switching between different elements, may simultaneously convey multiple messages (Gil & Gahr 2002).

Various methodological approaches, ranging from field and laboratory experiments to multi-species comparisons, improve our understanding of song functions. The latter approach may be especially useful for understanding the evolution of song signalling and key selection pressures affecting song performance among different species. To facilitate comparative studies, however, sufficient primary data are needed. Therefore, there is still a demand for descriptive studies on songs of taxa for which no or only basic song parameters are available.

A good description of a song structure and

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variation is also necessary for testing hypotheses about the function of song repertoires or syntax in species with complex songs. In our paper, we present a detailed description of songs of the tree pipit (*Anthus trivialis*, Motacillidae), which, as a common bird with a medium-sized repertoire and complex song, may become a good species for such studies.

The tree pipit is a widespread Palaearctic ground-breeding songbird, with very conspicuous male singing behaviour. Two major categories of tree pipit songs can be distinguished — songs from posts such as trees or other vegetation ("perched songs") or songs performed in flight ("flight songs"). Although songs of the latter category are less common, song flights are regular parts of the male behaviour, so characteristic that they are usually used for fast identification of this species in the field (Wallschläger 1984, Alström & Mild 2003, Šťastný *et al.* 2006).

Differences between flight and perched songs are common in many bird species (e.g., Ferry 1947, Sorjonen & Merilä 2000, Balsby & Dabelsteen 2003). In some of them, flight songs seem to serve primarily for mate attraction (e.g., Wittenberger 1983, Balsby & Dabelsteen 2003); in others they are used in male–male competition during the pre-mating period (Sorjonen & Merilä 2000) rather than presented to females. Males of tree pipits sing mostly during the period of territory establishment and pairing (Loske 1987b), so various alternatives of the function of their flight songs remain open.

Although different aspects of tree pipit ecology have been studied in detail, e.g., breeding biology (Meury 1989, Burton 2006), habitat selection (Loske 1987a, Kumstátová *et al.* 2004) or population ecology (van Hecke 1981), its singing behaviour and song functions remain understudied. A few papers mention singing behaviour of tree pipit by describing its seasonal occurrence and associated male behaviour (van Hecke 1979, Loske 1987b), but only three studies contain a song description of this species *per se*. Bjerke (1971) analysed songs of seven individuals by acoustic inspection, Wallschläger (1984) described sonograms of six males from three German and one Russian population in his bioacoustical contribution to the systematics of Palaearctic pipit species, and just recently, Panov *et al.* (2006) attempted to analyse the organisation of tree pipit songs in more details. The conclusions of the last paper are nevertheless strongly limited by the fact that the main analysis was based on songs of a single focal male, and the number of recordings used in the study to reveal general rules of song sequence organisation and evaluate individual and geographical variability was insufficient for wide generalisation. Regardless of low sample sizes, another weak point of all the above-mentioned studies is that the authors either completely ignored flight songs (Bjerke 1971) or did not present enough material to enable a quantitative comparison of the two song types (Wallschläger 1984, Panov *et al.* 2006).

In our study, we analysed songs of 90 tree pipit males from five different localities in the Czech Republic in order to (1) describe song structure and syntax rules, (2) evaluate basic among-individual and among-population differences in song characteristics, and (3) describe differences between flight and perched songs as the two apparently different aspects of singing behaviour. We focused on various characteristics describing the song variation, from the basic temporal and frequency parameters to those concerning song organisation. If song flights and perched songs are addressed to different recipients (i.e., mates and rivals), we may presume that the structure or composition of these two song types are under different selection pressures. We therefore looked particularly for characteristics which could signal male quality to females (such as specific syllables or phrases with high production costs) or which might affect territorial encounters (such as those useful in neighbour–stranger recognition).

Methods

Studied species

The tree pipit is a common small, short-lived, monogamous migratory songbird, living in most of Europe as well as in a large part of the Palaearctic. As a ground-breeder, it is cryptically coloured without sexual dimorphism. It breeds over most of the Czech Republic, from lowlands to the subalpine belt of mountains (Šťastný *et al.* 2006). The species typically breeds in sparse woodland, at the forest margins or in open areas with the presence of higher vegetation that serves as song-posts and look-outs. Most tree pipit males have one or two such favourite singing posts within the territory. Occasionally, these may be substituted by steep hill slopes (Kumstátová *et al.* 2004). Males delineate and defend their territories by singing during most of the breeding season, from their arrival (usually in the last decade of April at Czech localities) until the beginning of July (Cramp 1988, T. Petrusková pers. obs.).

Studied populations

Tree pipit songs were recorded during the years 2002 to 2005 at five different localities in the Czech Republic covering an altitudinal gradient from 360 to 1400 m a.s.l. At two of them, pipit habitat preferences had been previously studied in detail (Kumstátová *et al.* 2004). Distances between the localities ranged from 35 to 250 km (Fig. 1). Singing territorial males were searched for in suitable habitats, either throughout most of the area of the studied localities or along ca. 200 m wide transects.

The first studied locality "Šumava" (49.0°N, 13.6°E; altitude 960–1160 m) was located in the Šumava National Park (English toponym: Bohemian Forest), around the former village Knížecí Pláně abandoned in the 1950s. The main study area (3.6 km^2) was formed by meadows and pastures with scattered trees and bushes, surrounded by spruce forests. Tree pipits inhabited forest edges as well as open areas with the presence of grown trees. Their density in the main study area was 0.4 pairs/10 ha, but solitary males were also recorded at suitable patches farther apart.

The second locality "Oblík" (50.4°N, 13.8°E; 0.65 km^2, alt. 360–509 m) lies in the landscape protected area České středohoří (Bohemian Uplands). The study area was located around two steep conic volcanic hills: Oblík (alt. 509 m) and Srdov (alt. 481 m), in a very heterogeneous mosaic of diverse habitats: shrub-invaded meadows, abandoned orchards, rocky steppe, etc. Tree pipits concentrated in suitable habitats in the close vicinity of both hills; their population density was approximately 4.4 pairs/10 ha.

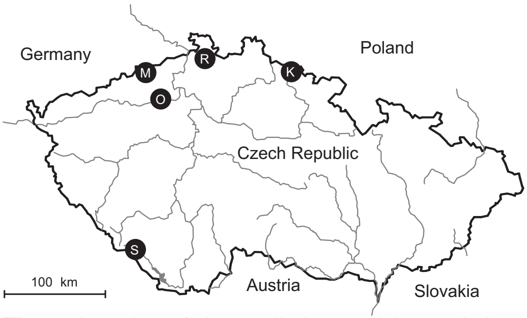

Fig. 1. Location of the studied tree pipit populations in the Czech Republic (major rivers in the country are shown). Each population (Krkonoše, Oblík, Šumava, Moldava, Rybniště) is indicated by its first letter.

The third locality "Moldava" (50.7°N, 13.7°E) was located in the Krušné hory (Ore Mountains). The study area (1.4 km^2, alt. 750–875 m) lies on a plateau around the hill Oldřišský vrch (alt. 875 m) near the village Moldava. It is relatively homogeneous, covered by intensive or extensive meadows, pastures, and abandoned fields intersected by streams. Tree pipits nest at suitable edges of the surrounding forested area or in abandoned fields overgrown by invading trees or shrubs. Their population density was approximately 0.4 pairs/10 ha.

The fourth locality "Rybniště" (50.9°N, 14.5°E; 3.4 km^2, alt. 450–470 m) lies at the edge of Lužické hory (Lusatian Mountains) among the settlements Rybniště, Horní Podluží and Krásná Lípa. It is a managed area with fields, intensive pastures and meadows intersected by lines or groups of trees, which are inhabited by tree pipits. Average density in the area was 0.5 pairs/10 ha, but at suitable places it could be an order of magnitude higher (1 pair per 2 ha).

The fifth locality "Krkonoše" (50.7°N, 15.6°E; alt. 1090–1350 m) was located in the mountain range Krkonoše (Giant Mountains). The region is mostly covered by spruce forest, at higher elevations by wet alpine meadows partially overgrown with sparsely growing spruce and dwarf pine. Tree pipits occurred there at open areas scattered among densely overgrown parts. Males were recorded along two linear transects, 4 and 1.3 km long, which followed the

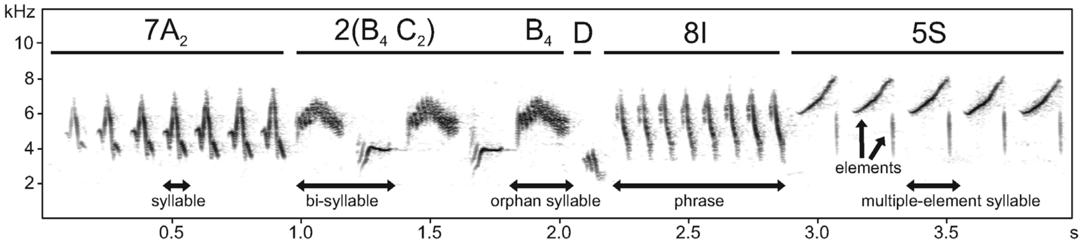

Fig. 2. Example of a tree pipit perched song (song code $7A_2$ $2(B_4\ C_2)B_4$ D 8I 5S) with indication of various structural features. Horizontal lines above the spectrogram indicate individual phrases.

most suitable habitats. The calculated population density of 1.1 pairs/10 ha therefore overestimates the average values for the area, although locally the density was even higher (3–6 pairs/10 ha).

Song recording

Birds were recorded between 06:00 and 18:00, with a Marantz PMD 222 recorder with a Sennheiser ME 67 shotgun microphone. Positions of all recorded males were marked on a map or aerial photograph of the respective locality. Beside the location of the subject male — to allow its unambiguous identification — we noted for each recording the time, behaviour of the subject (flight song = FS; perched song = PS) and the song-post characteristics. Most of the males were recorded during a single recording session.

All recordings were transferred from the Marantz PMD 222 recorder via a shielded analogue cable to a PC equipped with a Sound Blaster Audigy 2 Platinum sound card, and digitised using 44.1 kHz/16 bit sampling. Further analyses (sonogram inspection, time and frequency measurements) were performed with the Avisoft SASLab Pro 4.3x software (Specht 2007).

Syllable identification and terminology

The approach used for the basic analyses of tree pipit songs generally followed methods described in Osiejuk *et al.* (2003) and Rutkowska-Guz and Osiejuk (2004). Songs were described using syllables (defined as the smallest invariant units in a male's repertoire) as the minimal units of song production. Syllables were usually single-element sounds (Fig. 2); in some cases, however, units were present consisting of two or even more elements (the smallest continuous tracings on the sonogram) always occurring together (Fig. 2; *see* also songs 3 and 4 in Fig. 3b). We presume that these units represent a functional entity, and as such were treated as multi-element syllables. Syllables with the same shape on sonograms were assigned to the same syllable type, although they could differ, to some extent, in length and frequency among individuals and/or among performances.

To ensure reproducibility and reduce the effect of subjective errors, syllables were assigned to a particular syllable type in a two-stage procedure. First, a visual inspection of sonograms from all individuals was carried out, during which the database of sonograms of all syllable types was prepared. Syllables were assigned to a new type even if only small differences in sonogram shape were observed. However, we assumed that at this stage some categorisation could be imperfect because of (1) variable sound quality, (2) gradual variation within some syllable types, and (3) increasing experience of the person conducting the analysis.

Therefore, the initial categorisation of syllables was subsequently verified using the Avisoft SASLab "Scan for template spectrogram patterns" function, which is based on a spectrogram cross-correlation algorithm (Specht 2007), using the following settings: high-pass cut off frequency 1300 Hz, max frequency deviation 0 Hz, identification threshold 0.5–0.8 (depending on the quality of the recording), masking interval 0 s, margin 0.1 s. We used binary templates of visually identified syllable types to automatically classify sounds within the recorded material, and focused on apparently similar syllables to test whether their separation is justified. For each

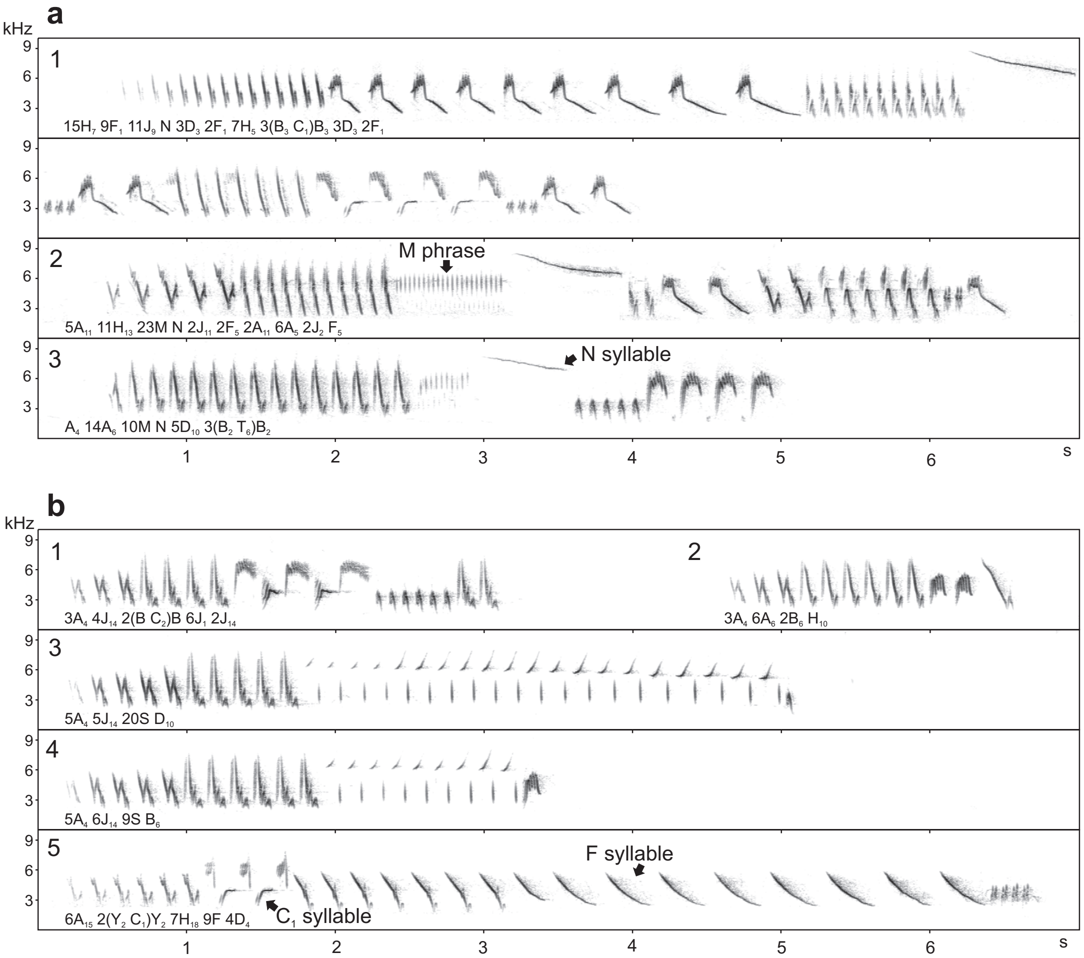

Fig. 3. Comparison of the structure of (**a**) flight songs and (**b**) perched songs. Individual songs are marked with numbers and their letter-number notation is shown. The most commonly occurring syllables are indicated with arrows.

group of similar but presumably distinct syllables, we scanned all recordings where any of these occurred, using templates of the respective syllables simultaneously. If classifications by two or more templates overlapped (both within and between recordings), these syllable types were pooled together. Conversely, if the classification within songs of individual males was always consistent but it differed among males, the syllable types in question were treated as distinct in further analyses. Each stage of the syllable classification (visual, template scanning) was done by a different person.

A typical feature of tree pipit songs is the regular occurrence of distinct combinations of two different syllable types in repetitions (Figs. 2 and 3). We presume that they are functionally similar to individual syllables, and use the term "bi-syllables" for such two-syllable combinations present in songs of one or more males. For repetitions of the same syllable of bi-syllable type within a song, we use the term "phrase". Bi-syllable phrases often begin or end with only one half of the respective bi-syllable; in such cases we regarded this "orphan syllable" as a part of the corresponding phrase (Fig. 2).

Song structure analysis

Although the tree pipit songs vary highly in duration, individual songs can be easily identified as they are separated by distinct gaps. Each song was analysed separately for the syllable content and order.

Syllable composition of the song was described by a symbolic letter-number notation; for example, the song in Fig. 2 was described as $7A_2$ $2(B_4$ $C_2)B_4$ D 8I 5S. Letters (often with subscripts) represent particular syllable types, two syllables in parentheses represent a bi-syllable, and preceding numbers indicate the number of repetitions of the particular syllable or bi-syllable type. These symbolic descriptions of individual songs were used as a source for the automatic calculation of further structural characteristics for each song (total number of syllables, number of different syllable and bi-syllable types, number of transitions, transition rate, syllable rate and versatility) as well as for summary statistics for each male and locality (presence and frequency of syllables and bi-syllables in the repertoire, occurrence of syllables at a particular position within songs). We defined "transitions" as switches between different syllable types within a song, and the "versatility" as the number of transitions divided by the maximal potential number of transitions in a song of a given length (i.e., number of syllables minus one). As both these characteristics could be strongly influenced by the number of bi-syllable repeats in a given song, we determined the "phrase versatility" in a similar way, focusing on switches between different phrases rather than different syllable types. The phrase versatility was therefore calculated as: (the number of phrases in a song)/[(number of syllables) – 1]. Transition, syllable and phrase rates were expressed as average numbers of transitions, syllables or phrases, respectively, per second.

We also measured spectral and temporal characteristics of all flight songs (which occurred more rarely) and of selected perched songs depending on the number of available recordings and their quality (on average 15 PS per male). Recordings were analysed with the Avisoft SASLab Pro 4.3x with the following set of parameters: FFT-length 512, Frame 100%, Hamming Window, Temporal Overlap 87.5%. This resulted in a 112 Hz bandwidth with 86 Hz frequency and 1.4512 ms temporal resolution. We manually measured maximal and minimal frequencies, bandwidth and duration. Additionally, we determined frequency at maximum amplitude (peak frequency), using the linear amplitude spectrum function with the Hamming evaluation window, 0.336 Hz resolution and the bandwidth threshold set to −20 dB.

Statistical analysis

Most statistical analyses were performed with the SPSS 12 PL software. Parametric or non-parametric tests (two-tailed) were selected depending on the conformance to normal distribution. To keep the type I error constant ($\alpha = 0.05$), we used the Bonferroni correction if multiple tests of similar null hypotheses were carried out. As the number of recorded songs differed among males, we used mean values of male song characteristics in tests to avoid pseudoreplication.

We conducted discriminant analyses to check whether individual songs can be classified as either PS or FS based on their structural characteristics (number of syllables and phrases, versatility, etc.), spectral characteristics (song duration, maximal and peak frequencies, bandwidth, etc.) or both. A cross-validation procedure (based on calculation of the discrimination omitting individual songs) was performed to check the success of classification.

The capture-recapture method was applied for estimation of the syllable repertoire size, using ComDyn4 (Community Dynamics software by Jim Hines, www.mbr-pwrc.usgs.gov), which was developed to estimate parameters associated with community dynamics using presence/absence data (Boulinier *et al.* 1998). In our case, we estimated an equivalent of the species richness, i.e., the syllable repertoire size of each male, for which we had data on presence/absence of particular elements in songs. The basic estimator for species richness in ComDyn4 is the jackknife estimator proposed by Burnham and Overton (1978, 1979), which was shown to be reasonably robust to potential departures from model assumptions and has performed well in several studies (Garamszegi *et al.* 2002, 2005, Bell *et al.* 2004). For perched songs, we estimated PS syllable repertoire size of each male for which at least 20 PS were available; this estimate was based on the first 20 PS of each such male. This value seems to be sufficient for repertoire size estimation in various bird species (Garamszegi *et al.* 2005). As the flight songs were relatively rare, we estimated FS syllable repertoire size only for males with four or more (up to seven) recorded FS, using all available FS.

Results

The analysed material consisted of 2166 songs recorded from 90 males at the five studied localities. On average, we recorded 24 songs per male; averages and ranges per locality are given in Table 1. In total, we distinguished 153 different syllable types, out of which 114 (74.5%) were unique for a single locality. Remaining syllables were shared among two (27 syllables; 17.6%), three (5; 3.3%), four (3; 2%) or all (4; 2.6%) localities. More details on syllable and bi-syllable types found at the different localities, and of male repertoires, are presented in Table 1.

Structure and frequency characteristics of flight and perched songs

We found that flight songs (FS) and perched songs (PS) significantly differed in most measured characteristics (Table 2). FS were characterised by wider bandwidth, which was mostly linked with higher maximal frequencies of such songs. On the other hand, minimal frequencies were only slightly lower in FS, and peak frequencies between both types of songs did not differ significantly. We observed highly significant differences in duration and syllable composition of these two song categories. FS were typically longer, which was reflected in a significantly higher number of syllables (on average almost double) and phrases (1.5 times more) than in PS. On average FS also contained almost twice as many different syllable types. However, average phrases in PS were slightly shorter than in FS (as seen in a higher phrase rate) and commonly contained bi-syllables, which was reflected in both higher versatility and higher phrase versatility of PS.

In the discriminant analyses based on (1)

Table 1. Basic data on analysed song material. Variables for which the variation is expressed by averages and ranges (given in parentheses) were calculated across all males in the given locality, repertoires were calculated from all songs recorded at the locality.

Locality	No. of males	Total no. of songs	Recorded songs per male	Proportion (%) of FS of all songs	Syllable types per locality	Unique syllables per locality	Individual syllable repertoires	Bi-syllable types per locality	Unique bi-syllables per locality	Individual bi-syllable repertoires
Krkonoše	15	350	23 (8–39)	11 (0–22)	57	34	10.5 (5–18)	16	14	1.8 (1–5)
Oblík	13	404	31 (9–64)	10 (0–28)	31	13	12.8 (9–15)	15	12	3.1 (1–5)
Šumava	39	892	23 (5–51)	8 (0–25)	60	35	11.2 (3–17)	22	19	1.5 (0–3)
Moldava	12	308	26 (8–48)	7 (0–31)	35	12	11.9 (8–18)	11	7	1.3 (0–3)
Rybniště	11	212	19 (10–33)	6 (0–20)	32	20	11.2 (7–16)	7	6	2.7 (1–4)

spectral and temporal characteristics, (2) structural characteristics, or (3) these two sets combined, we extracted a single canonical factor for the separation of flight and perched songs. The results of all analyses were very similar, especially in the assignment of flight songs (87.8–88.6% of correct classification in the cross-validation procedure). The proportion of correct assignment of perched songs varied slightly more: the first discrimination, based solely on spectral and temporal characteristics, classified 89.4% of 176 FS and 1413 PS correctly in the cross-validation procedure; this represented a correct assignment of 89.5% of PS. The parameters that loaded highest were song duration, maximum frequency, and bandwidth. In the second discriminant analysis, we used structural characteristics calculated for all recorded songs (181 FS, 1985 PS). In this case, the cross-validation procedure assigned 93.3% of songs correctly to FS or PS (93.8% correctly classified PS); the highest-loading variables were number of syllables and number of different syllables. Pooling structural and spectral characteristics together did not improve discrimination substantially (93.7% correct assignments in the cross-validation procedure; 94.3% PS).

Variation in basic song parameters among localities

Several song characteristics, especially those related to the song complexity, differed significantly among localities (FS and PS were compared separately with ANOVA or Kruskal-Wallis ANOVA, all P values shown are after Bonferroni correction): bi-syllable repertoire size (PS: $P < 0.05$), number of transitions (PS: $P < 0.01$; FS: $P < 0.001$), versatility (PS: $P < 0.001$; FS: $P < 0.05$), syllable rate (PS: $P < 0.05$), and transition rate (PS: $P < 0.001$). The post-hoc analyses revealed that these differences concerned PS of males from Rybniště, which were more complex (higher values of versatility, transitions, etc.) than those from other localities. Additionally, the duration of flight songs also significantly differed among localities ($P < 0.05$); FS from Rybniště (mean duration 8.5 ± 0.9 s) and Krkonoše (7.9 ± 0.5 s) were on average longer in comparison to those from other sites (mean duration 5.7 to 6.2 s).

To test for significant differences in repertoire size among localities, we used an ANOVA model with repertoire size as a response variable, locality as a factor and number of songs recorded per male as a covariate. We did not find any significant difference in syllable repertoire size

Table 2. Comparison of characteristics of perched and flight songs of tree pipit males. Means (± SE) were calculated based on average male parameters. Paired tests (*t*-test or Wilcoxon Signed-rank test) were calculated depending on the conformance to normal distribution.

Song variable	Flight song	Perched song	*N* males	Statistics	Significance after Bonferroni correction
No. of syllables	50.4 ± 1.81	19.9 ± 0.58	73	$t = 16.51$	$P < 0.001$
Different syllable types	6.2 ± 0.17	3.7 ± 0.08	73	$t = 13.79$	$P < 0.001$
Different bi-syllable types	0.61 ± 0.057	0.61 ± 0.037	73	$Z = 0.26$	ns
Transitions	11.0 ± 0.9	6.4 ± 0.34	73	$t = 5.13$	$P < 0.001$
Versatility	0.22 ± 0.016	0.33 ± 0.014	73	$t = -6.23$	$P < 0.001$
Duration	6.46 ± 0.246	2.44 ± 0.125	74	$t = 14.06$	$P < 0.001$
Syllable rate	8.25 ± 0.239	6.72 ± 0.091	73	$t = 6.10$	$P < 0.001$
Transition rate	1.64 ± 0.099	2.06 ± 0.097	73	$t = -3.36$	$P < 0.01$
Min frequency	2.11 ± 0.021	2.23 ± 0.016	74	$t = -6.52$	$P < 0.001$
Max frequency	8.11 ± 0.059	7.33 ± 0.036	74	$t = 14.35$	$P < 0.001$
Bandwidth	5.96 ± 0.076	3.95 ± 0.142	74	$t = 11.74$	$P < 0.001$
Peak frequency	4.11 ± 0.077	4.28 ± 0.046	73	$t = -2.22$	ns
No. of phrases	5.40 ± 0.265	3.45 ± 0.084	73	$t = -6.68$	$P < 0.001$
Different phrases	4.66 ± 0.181	3.22 ± 0.072	73	$t = -6.85$	$P < 0.001$
Phrase versatility	0.116 ± 0.0045	0.130 ± 0.0041	73	$t = 3.15$	$P < 0.05$
Phrase rate	0.87 ± 0.037	1.28 ± 0.040	73	$t = 7.02$	$P < 0.001$

among localities ($F_{4,84} = 0.827$, $P = 0.511$), but the number of songs recorded was found to significantly affect the observed repertoire size ($F_{4,89} = 5.395$, $P = 0.023$). As the bi-syllable repertoire size did not conform to normal distribution, we used the Kruskal-Wallis ANOVA to test for differences among localities. These were highly significant ($\chi^2 = 31.139$, df = 4, $P < 0.001$); males from Oblík and Rybniště had more different bi-syllables within their repertoires (median = 3, means ± SE: 3.08 ± 0.265 and 2.80 ± 0.327, respectively) than males from Šumava (median = 2, mean ± SE = 1.53 ± 0.113), Krkonoše and Moldava (median = 1, mean ± SE: 1.80 ± 0.296 and 1.25 ± 0.218, respectively).

Observed versus estimated syllable repertoire size

To characterise the overall repertoire size of tree pipit males, we initially calculated the number of different syllable types and bi-syllables recorded per male (Table 3). The syllable repertoire size was significantly correlated with the number of songs recorded per male ($r = 0.28$, $P = 0.007$, $n = 90$), while the bi-syllable repertoire size seemed not to be affected by the number of songs recorded ($r_s = 0.09$, $p = 0.38$). Therefore, we used the capture-recapture approach (*see* Methods) to estimate the real syllable repertoire size or included number of songs recorded per male as covariates in further analyses.

Significant correlations between the observed syllable repertoire and sample size suggest that simple counting of different syllables from a relatively small number of songs per male could underestimate the real syllable repertoire size. We therefore used the species richness concept to estimate syllable repertoire size based on the syllable presence/absence within subsequent songs of a male. For PS, we compared observed and estimated repertoire sizes for males for which we had 20 or more PS recorded ($n = 47$). The observed syllable repertoire size within the first 20 songs ranged from 6 to 20 (mean ± SE = 10.2 ± 0.39), and the estimated repertoire size was between 6 and 24 (mean ± SE = 10.9 ± 0.49). The difference between observed and estimated repertoire size, though small, was significant (paired *t*-test: $t = -3.874$, df = 46, $P < 0.001$). As the FS were much rarer, we used only recordings of those males for which we had four or more FS recorded ($n = 16$). The observed syllable repertoire size of these males ranged from 7 to 12 (mean ± SE = 9.6 ± 0.41), and the estimated repertoire size from 7 to 20 (mean ± SE = 10.5 ± 0.76). The estimated values were on average slightly higher than observed ones; however, this difference was not significant, likely due to a small sample size ($t = -1.86$, $P = 0.083$).

Within-male differences in estimated syllable repertoire size of FS and PS were not significant (Wilcoxon signed-rank test: $Z = -0.288$, $n = 16$, $P = 0.774$). For this comparison, we used estimates from all 16 males where at least four FS were available, using all FS (4 to 7) and up to 20 subsequent PS (for three males, we had fewer numbers of PS available: 9, 13 and 18).

Patterns of within-song syllable use

There was a high variation in local dialects among the studied populations, reflected by a substantial proportion of syllable types unique for one population only (Table 1). The regional variability in repertoires will be the focus of a separate manuscript; presently we will discuss some general patterns in syllable use. Only four out of 153 syllable types were found in the repertoires of at least some males from all five localities: C_1, F, M and N (for their spectrograms, *see* Fig. 3). C_1 and F occurred frequently both in

Table 3. Syllable and bi-syllable repertoire sizes (ranges and means ± SE) within flight and perched songs.

	Syllable types	Bi-syllable types
All songs (*n* = 90 males)	3–18 (11.4 ± 0.30)	0–5 (1.9 ± 0.11)
Flight songs (*n* = 73 males)	3–15 (7.7 ± 0.30)	0–3 (0.88 ± 0.10)
Perched songs (*n* = 90 males)	3–17 (10.0 ± 0.27)	0–5 (1.8 ± 0.11)

flight and perched songs, the two other types were present substantially more often in FS. The M syllable occurred in 83% of 181 analysed flight songs but only in 3% of 1985 perched songs; this pattern was even more pronounced for the N syllable (85% *vs.* 1.3%). Following each other as an M–N sequence, these syllables were present exclusively in flight songs (in 73% of them), usually in the middle of a complete FS (Fig. 3a). The pattern of occurrence of the M syllable was particularly interesting. This syllable was repeated in a high-rate phrase (i.e., trill), and varied greatly in length among males (from four repeats in three different flight songs of one male from Oblík to 45 repeats in FS of a male from Rybniště; on average, flight songs with the M syllable contained 21 repeats of M).

The F syllable was relatively common; we found it in 35% of all FS and in 14.4% of all PS recorded. However, it differed in position within PS and FS; in PS it was mostly present as the final syllable type (in 85% of 285 PS containing F), while in FS it was commonly present in the middle of the song (in 53% of 64 FS containing F). The F syllable never occurred at the beginning of a song.

The C_1 syllable was almost exclusively found as a part of bi-syllables, and almost one third of all different bi-syllables types contained C_1. With one exception (2 songs of the same male out of 363 songs containing C_1), it was never used as the first syllable in a song.

The majority of males started their songs with a certain dominant phrase, usually a repetition of one syllable or sometimes bi-syllable type: 59% of males used only a single type of "introductory phrase" in all of their recorded songs, in 82% of males such a dominant phrase was found at the beginning of at least 75% of their songs. This pattern was consistent for PS as well as for FS. The most preferred introductory syllables varied among localities (reflecting the variation of local dialects). Several males at one locality often shared the same dominant introductory syllable but the level of such sharing varied greatly among localities (Table 4). Phrases following the introductory ones ("second phrase") no longer seemed to follow any consistent pattern — there was much higher variability within songs of the same male, and only rarely any syllable or bi-syllable type clearly dominated over the others (Fig. 4).

Bi-syllable repertoires varied greatly among males, and showed a high degree of individuality. Out of 64 different bi-syllable types, more than half (34, i.e., 53%) were recorded uniquely in the repertoire of a single bird, and only eight bi-syllable types were shared by more than five males. The most widespread bi-syllable — I_2 J_2 — was shared by 16 birds from three localities; twelve of these males, however, were from a single place (Oblík).

Discussion

In this study, for the first time we present the data on the tree pipit song organisation, repertoire size and among-population differences based on a large number of recordings. In contrast to previous studies (Bjerke 1971, Wallschläger 1984, Panov *et al.* 2006), our material covered individual, intrapopulation, as well as regional variation. We provide evidence for differences in the structure of songs performed from perches and in flight. Clear among-population differences were observed as well, mostly involving sharing of introductory syllables (likely a dialect pattern), but to some extent also song duration and complexity. We also located specific song structures, which may be potentially important for individual recognition (bi-syllables) or advertising male quality (M-phrase).

Table 4. Proportion (%) of males using the same dominant introductory phrases at the studied localities. Except for Rybniště where all four are indicated, only the two most common introductory syllables are listed per locality.

	Krkonoše		Oblík		Šumava		Moldava		Rybniště	
Most common	H_1	47%	A_{17}	38%	A_4	55%	A_2	92%	H_{15}	36%
Second	A_3	13%	A_{15}	38%	A_2	18%	H_{15}	8%	A_{18} & A_{20}	27%
Sum of remaining types	Σ of 6	40%	Σ of 2	24%	Σ of 5	27%			W_1	9%

Flight and perched songs: structural differences and possible functions

Tree pipit songs varied highly in duration, both among different performances of one male and among males; variable song length was appropriately reflected in the total number of syllables, and to some extent in the within-song repertoire size (i.e., the number of different syllables). This observed high variability is in accordance with the scarce data already available (Cramp 1988, Alström & Mild 2003, Panov *et al*. 2006). Frequency-based parameters were more consistent throughout recorded songs, and sonograms presented in other publications (Wallschläger 1984, Cramp 1988, Alström & Mild 2003, Panov *et al*. 2006) show that these parameters are relatively stable over a much larger area than covered by our study. Lower frequency of FS in comparison with PS also seems to be a general pattern for the studied species (Cramp 1988, Panov *et al*. 2006).

Although almost all evaluated parameters differed significantly between flight and perched songs, the most interesting differences are apparently those concerning duration and syllable composition. FS were significantly longer, consisted of about twice as many syllables (as well as different syllable types), but on average contained longer phrases, which was reflected in lower versatilities. Analysed FS of tree pipits showed higher syntax consistency than PS. The most obvious was the occurrence of two syllable types — M and N — that were common in most FS but present only rarely in PS; in combination we found them only in FS (Fig. 3a). This M–N sequence seems to be conservative; it was present in sonograms from England (Cramp 1988), Russia (Wallschläger 1984, Panov *et al*. 2006) and Germany (Wallschläger 1984). Contrary to our results, however, the one male analysed in detail by Panov *et al*. (2006) apparently also used the M–N sequence in perched songs.

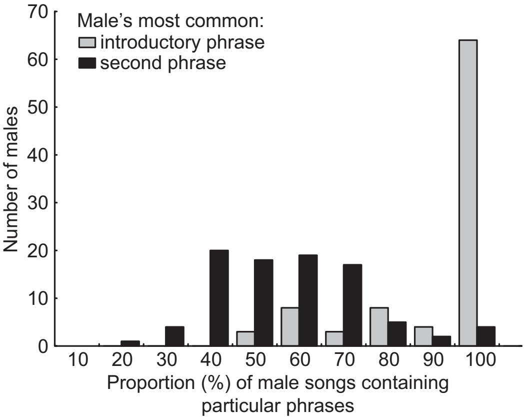

Fig. 4. Frequencies of the most common introductory (first) and second phrases of recorded males. For each male, a phrase most commonly occurring at the first position within songs was selected, and the frequency of songs beginning with such phrase was calculated. The frequency of "second phrases" within songs was calculated accordingly.

The differences between PS and FS suggest that these song categories might diverge in their functions. Some studies have linked differences between PS and FS to their functions in either inter- or intrasexual selection processes. In various birds, FS seem to be directed mostly to females and PS to rival males (Whittenberger 1983, Ammer & Capp 1999, Balsby & Dabelsteen 2003). However, in other species FS are used primarily in territorial defence (Conrads 1969, Sorjonen & Merilä 2000).

Like in most pipit species with complex songs, PS of tree pipits are usually incomplete versions of FS (Alström & Mild 2003). Observations of van Hecke (1979) suggest that both song types are used in male–male interactions during territory establishment: in the presence of another male, the territory owner gradually changed behaviour — first it increased the PS rate, subsequently performed FS, and eventually attempted to chase the intruder away. Similar behaviour was described for closely related meadow pipits *Anthus pratensis* (Ferry 1947), and FS was considered to mark territory boundaries in water pipits *A. spinoletta* and red-throated pipits *A. cervinus* (Cramp 1988).

On the other hand, it has also been suggested that tree pipit FS may have a mate-attracting function (Seel & Walton 1979). Unpaired tree pipit males certainly tend to sing more than paired ones (Loske 1987b, T. Petrusková, pers. obs.), and more frequent FS performance among unpaired males was described for rock pipits *A. petrosus* (Askenmo *et al*. 1992). FS of tree pipits are longer and more complex (consisting of a higher number of syllable types than PS), and several studies have shown that increased song complexity might be an effect of stronger intersexual selection (Searcy 1990, Ammer & Capp 1999, Balsby & Dabelsteen 2003, Ballentine *et al.* 2003). Additionally, tree pipit FS more frequently contained the M phrase, which strongly varied in duration among males. Such a fast-rate trill structure is probably physically demanding (Podos 1997) and similar phrases have been shown to play an important role in female choice in various birds (Vallet *et al.* 1998, Balletine *et al.* 2004). However, trills may be used also for intrasexual assessment of competitor quality (Illes *et al.* 2006), and the relatively infrequent occurrence of FS makes this song type unlikely to be primarily directed toward females, which may evaluate males by song complexity.

The potential differences in function between PS and FS of tree pipits therefore remain unclear. We may presume that PS are more likely directed to neighbouring males, while FS may act as a stronger signal of male quality both intrasexually and intersexually. To test for specific hypotheses on the FS function, studies focusing on temporal variation of flight song use across a season and in a specific context (paired *vs.* unpaired males) may be designed.

Species, local dialect and individual recognition

A bird song is usually a multiple-character signal, in which more than one type of information is encoded (Gil & Gahr 2002). Regardless of whether they are primarily for attracting mates or deterring rivals, songs in many species simultaneously carry information enabling: (1) species recognition at a distance (Elfström 1990, Baker 1991, Mathevon & Aubin 2001), (2) discrimination between birds singing local and foreign dialects (Nelson & Soha 2004, Osiejuk *et al.* 2007), and (3) discriminating between neighbours and strangers (Molles & Vehrencamp 2001, Skierczyński *et al.* 2007) or even among individual neighbours from a local population (e.g., Stoddard *et al.* 1991).

Closely related pipit species, such as tree and meadow pipits, have often very similar morphology and ecology, and they coexist at some localities (Kumstátová *et al.* 2004, Šťastný *et al.* 2006). The song may therefore play a crucial role in species recognition. Tree and meadow pipits discriminate very well between conspecific and heterospecific songs in playback experiments (Petrusková *et al.* 2008). The mechanisms of species recognition, however, likely differ among various pipit species. Elfström (1990) showed that very similar songs of meadow and rock pipits have two distinct parts, the first being highly variable and used for individual identification, while the second, more consistent part is apparently useful for species recognition. Within tree pipit songs, we also found relatively stable parts (introductory phrases) among males from individual populations; however, the among-population variability of such phrases was high (Table 4), so it is more likely that such song structures are associated with dialect rather than species recognition.

The comparison of songs from different Czech populations and from other studies presenting sonograms (Wallschläger 1984, Cramp 1988, Alström & Mild 2003, Panov *et al.* 2006) suggests that species-specific recognition might be more related to similar overall frequency characteristics of tree pipit songs, rate of syllable delivery or the widespread occurrence of certain similar syllable types. Apart from the characteristic M–N sequence within complete song flights, elements similar to the syllable F frequently found in Czech populations are easy to recognise on sonograms obtained from other, even very distant populations (Wallschläger 1984, Cramp 1988, Alström & Mild 2003, Panov *et al.* 2006). However, our data clearly show the existence of local dialects among tree pipit populations — the syllable repertoires of males from different populations are in general quite variable, and there was a relatively large proportion of syllables used uniquely in one of the studied populations.

In contrast to the tendency to share introductory phrases within populations, we found great individual variability in the use of bi-syllables. Although males varied greatly in syllable repertoire sizes, their bi-syllable repertoires were much smaller and more stable (on average 1.9 ± 0.11 bi-syllable types per male), and more than half of the bi-syllables recorded in our study were used solely by one male. Detailed analysis of bi-syllable functions requires further investigation; however, we may presume that bi-syllables can play an important role in individual recognition, while introductory syllables might contribute to the recognition of local dialects, i.e., for discrimination between local birds and strangers.

Conclusions

The detailed description of tree pipit song characteristics enhances the potential to use this common and widespread species as a model for studying song variation and function in birds with complex repertoires. This will allow future studies to focus in more detail on various aspects, such as regional variation, the adaptive function of certain song elements (e.g., M trills) or on the general rules of syntax within such songs.

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