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Song structure and repertoire sharing in the Tawny Pipit *Anthus campestris* in Poland

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Abstract. The present study characterizes the song of Tawny Pipit males (n = 55) recorded in May 2005 in the Wielkopolska region of Poland. Tawny Pipits sang with a very variable rate of 4-28 songs per minute (mean ± SE 16.0 ± 1.35). Songs were thus short, with an average duration of under 0.5 sec. At the same time, songs were relatively complex in structure and consisted of 2–3 (max. 5) units of frequency between 2.7 and 5.3 kHz. Based on visual inspection of sonograms and further cross-correlation analysis, 20 different song types were distinguished. Each male had only a single song type in his repertoire and the rendition of strophes produced by a male were very stereotypical. The songs of different males exhibited varying levels of similarity, from completely different, through sharing some within-song units, to strongly similar on sonograms. However, even the strongly similar songs of different males demonstrated some individuality in frequency parameters or fine note structure. On average, there were only 0.38 different song types per male within the population studied, and 83% of males sang song types shared with at least one other male. Nine of the 20 song types described were unique, i.e. sung by single males. The results of this study suggest that a highly variable song rate may be a signal of male motivation, whereas individual differences in song structure probably enable individual recognition.

Key words: Tawny Pipit, *Anthus campestris*, song structure, song rate, repertoire sharing, small repertoire size

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INTRODUCTION

Bird song is a sexually selected trait of critical importance to mate attraction and territorial defence. In songbirds (Oscines) song is culturally transmitted through learning and, as a signal, has a multidimensional character. Birds may change several aspects of their vocalization at a time, e.g. amplitude, rate, frequency, specific syllable contents etc. (Catchpole & Slater 1995, Gil & Gahr 2002, Brenowitz & Beecher 2005). Consequently, we observe numerous song strategies among species and the same song functions are often fulfilled in different ways. For example, in some species females are attracted by special sexy syllables (Draganoiu 2002) while in others different aspects are important e.g. repertoire size (Hasselquist et al. 1996). Also, the second function of song — territorial defence — is accomplished with different acoustic "tools", e.g. rival males are deterred by song type matching (Beecher et al. 2000), overlapping rival's songs (Osiejuk et al. 2007b) or song type switching (Osiejuk et al. 2007a). Consequently, despite the fact that our knowledge of song behaviour has increased substantially in the last fifty years, several questions remain unanswered. One of these gaps in knowledge concerns songbirds with small repertoires, and factors affecting changes in repertoire size on an evolutionary scale (Slater 2003). To answer questions such as Why do some related bird species have small repertoires or simple songs while others do not? we need reliable data on the bird's phylogeny, mating system, ecology and primarily on their song behaviour. Unfortunately, most of studies in bioacoustics were done on a relatively small number of model species (Catchpole & Slater 1995).

Pipits are from the genus *Anthus* which contains over 40 species with a widespread distribution around the world, and contain species with both very simple and complex songs. Thus it seems to be an ideal group for testing evolutionary hypotheses related to song (Alström & Mild 2003). The problem is that we still lack fundamental data on song behaviour in this group, even for some common European species (see Petrusková et al. in prep.). This paper aims to fill one of these gaps.

The Tawny Pipit is one such pipit species for which we have only scattered data, based on small sample size information on song behaviour (Neuschultz 1986, Cramp 1988, Thirion & Lebon 2006). Tawny Pipits choose exposed song posts or sing in flight (Krüger 1989, Voelker 2001). Males are known to have single song type repertoire and each has its own song type which is distinguishable from others (according to Neuschultz 1986). In this paper we present data on Tawny Pipit song from an area where species density is among the highest in Europe (Grzybek et al. in press). We focused on such aspects of song as the structure of strophes, rate of song delivery, and song sharing pattern within the local population. The main aim of this study was to provide general information about the song of the Tawny Pipit in the dry farmland landscape of central Poland and to compare this with other populations.

STUDY AREA AND METHODS

Study area

The sound records were collected near the town of Koło, in the Wielkopolska region, Poland (area 100 km^2, 52°12′N, 18°39′E). The study area was situated in an agricultural region with arable fields, meadows and small woodlots containing varying numbers and ages of trees. The soil is of very low quality, with a high percentage of sand and gravel fragments not used by farmers. Another characteristic of the study area are brown coal mines, either still in use or re-cultivated, as well as large gravel pits. The density of breeding pairs on the plot was high — 85 territories/100 km^2 (Grzybek et al. in press). For more details on the habitat structure of territories, as well as aspects of breeding ecology see Grzybek et al. (in press).

Recording

Birds were recorded between 10th and 25th May 2005, using a Sony TCD-D8 DAT recorder with a Sennheiser ME 67 shotgun microphone. In addition to the location of the subject male, each recording was given an unique number and the following notes: time, behaviour of the subject (song, calls etc.), context status (counter-singing, solo singing), and song post characteristics (sitting place, height of sitting place, distance to an open area).

Song analysis and bioacoustics terminology used

All recordings were digitally transferred from a Technics SV-DA10 recorder via a SPDIF cable to a PC workstation with RME Hammerfall DSP Multiface and PCI interface using 48 kHz/16 bit sampling. Initially, recordings were visually inspected in Avisoft SASLab Pro 4.39 software with the following set of parameters: 1024 FFT-length, Frame [%] = 25, Window = Hamming and Temporal Overlap = 87.5%. This gave a 244 Hz bandwidth with 42 Hz frequency and 2.9 ms time resolution (Specht 2002). For the detailed measurements of frequency parameters of songs we used a One-dimensional Transformation function called Amplitude spectrum (linear) with Hamming evaluation window (bandwidth 1.782 Hz and resolution 0.732 Hz). Using this function, we measured eight variables (Table 1). For bandwidth-related measurements, the Spectral Characteristics option "total" was on and the minimum frequency range was limited to 1.5 kHz to remove background noise. For more details on measurement characteristics see Specht (2002).

There were relatively few other species singing in the background in our recordings, therefore we used a semi-automated method of extracting Tawny Pipit songs for further analysis. As this is a new approach enabled by some new functions of bioacoustics software, we have described it here in detail. First, all recordings were joined together into a single WAV file of over 1 GB, with visible (on sonograms) breaks between original tracks indicated by inserted synthetic sounds. After visually inspecting the songs we found that most Tawny Pipit songs had a minimal frequency well above 2 kHz. Therefore, we filtered the WAV file using Avisoft Time Domain FIR-filter with 1.5 kHz highpass setting. Then we created labels using Avisoft 'Create section labels from waveform events' with the safe settings (threshold: 0.01 V, hold time: 0.5, margin: 0.5 s), which enable detecting and labelling all Tawny Pipit songs. Then we cut out all unlabelled sections with Avisoft function 'Save all labelled sections into single .wav file', which enabled us to compress the file (remove silent parts) by ca. 70% and separate the following songs sung by a particular male by small

(1–2 s) gaps. We then conducted a visual inspection of the sonograms in order to detect all possible different song types sung by all recorded males. At this stage we intentionally did not avoid redundancy, and each song which appeared to be visually different in structure on the sonogram was given its own name (e.g. A, B, C...) and particular examples of these song types were given numbers (e.g. A1, A2, A3 are the A song types of three different males). These were cut and inserted into a separate file (template file). The template file contained ca. 60 songs, which were roughly categorized into 21 different types.

The next stage of analysis was done with the XBAT (PREVIEW REVISION 4, H. Figueroa, www.xbat.org). Based on a template file we prepared in XBAT a so-called presets file, which contained all earlier visually selected song templates. We then opened in XBAT the original file with all recordings joined together and ran an automatic detection using the templates saved in our presets. We used a default 0.4 correlation threshold for automatic detection. We then visually inspected the file again, removing obviously wrong detections and adding some undetected (poor quality) songs. Altogether the manual correction of the final results concerned less than 1% of the songs. Based on these analyses we calculated the number of songs sung by different males, the average rate of singing and we have chosen the best quality songs for further analyses, which were conducted in Avisoft SASLab Pro. The method allowed rapid initial visual classification of the songs, in a compressed file and enabled the verification of visual song type classification in all recordings with an objective and fast correlation algorithm of XBAT.

Sound material

Birds were recorded on 38 sites and we recorded a total of 55 males. On nine sites more than one bird singing (or calling) was recorded, but it was not always possible to obtain good samples of songs from all males within such sites. In 15 cases males were calling and some of them gave only calls, therefore the song repertoire of these males remained unknown. Our sample consists of 218 recordings, which contain 2541 songs and 219 calls (not analysed here). We recorded 46 ± 8.0 (mean ± SE) songs per male (range: 1–278). In some cases it was not possible to measure all of the song parameters, e.g. because of recording quality or background noise, so the sample sizes may differ between analyses.

To test if our sample size was large enough to estimate song type repertoire at the population level, we used the species richness concept with model M(h) using program ComDyn4/SpecRich2 (http://www.mbrpwr.usgs.gov/softwar/specrich2.html, White et al. 1978, Rexstad & Burnham 1991). All statistical calculations were performed using SPSS v. 12 PL software.

RESULTS

Song rate and structure

Tawny Pipit males sang with an average rate of 16.0 ± 1.35 (mean ± SE) songs per minute, varying between 4.3 and 28.5 songs per minute. Only longer recordings (duration ≥ 1 min) of solo singing males were included in this analysis (n = 23). There was no significant correlation between song rate and recording duration for the recordings included in the analysis (r = 0.14, p = 0.523).

Table 1. Basic parameters of Tawny Pipit song from the studied population. For the estimates, we used the single best quality example of each song type described from 53 males.

Song variable	Variable descriptions	Min–Max	Mean ± SE
DURATION [ms]	Duration of the whole song	272–657	440 ± 9.9
FMA [Hz]	Frequency of maximal amplitude	3008–4989	4152 ± 65.1
L25 [Hz]	Frequency below which 25% of the total signal energy is distributed	3156–4142	3600 ± 32.9
M50 [Hz]	Frequency below which 50% of the total energy is distributed	3505–4729	4154 ± 33.9
U75 [Hz]	Frequency below which 75% of the total signal energy is distributed	4248–5646	4793 ±47.6
MINF [Hz]	Minimum frequency measured for -20 dB threshold	1976–3916	2700 ± 60.3
MAXF [Hz]	Maximum frequency measured for -20 dB threshold	4586–4464	5346 ± 60.9
BANDWIDTH [Hz]	MAXF – MINF	965–4464	2646 ± 102.0

Songs of the Tawny Pipit were short, with an average duration of less than 0.5 sec (Table 1). Additionally, songs were relatively complex and consisted of 2–3, or even up to 5, units. In several song types described, males simultaneously produced two sounds with different fundamental frequencies and with different frequency or amplitude modulation patterns (Fig. 1). This suggests that males simultaneously and independently use both parts of their syrinx to produce songs. Another aspect of song complexity revealed that within a few song types some larger units consisted of several very short notes, tightly packed in time (e.g. song type B, see below). Predominantly, the frequency of songs varied between 2.7 and 5.3 kHz with the most energy produced at the 4.1 kHz level (Table 1). None of the song frequency parameters were significantly correlated with their duration.

Song type repertoire and repertoire sharing

Based on a visual inspection of the sonograms, 21 different song types were originally distinguished. However, further correlation analysis in XBAT revealed that one of the song types described as new was only a poorer quality example of a type distinguished earlier. Detailed analysis confirmed that all the males recorded in the studied population had a repertoire of a single song type. Twenty different song types found within the studied population had similar multiple characteristics (Table 1). Some of the described song types had a completely different structure, i.e. sharing no unit(s) within a strophe (e.g. first four songs from Fig. 1). Some of the song types described had at least one shared unit(s) within a strophe and therefore could be classified as belonging to the same category of song types (Fig. 2). Finally, several males sung song types which were roughly the same (Fig. 3 and 4). We found that subsequent renditions of songs from a particular individual were very similar in duration and structure. On the contrary, songs classified as belonging to the same song type but sung by different males had small but consistent differences, which concerned both timing and energy distribution in the frequency domain. In some cases it was easy to identify small differences in acoustic structure which concern subunit structure (compare song types A and B of different males, Fig. 3 and 4).

Table 2. General Linear Models explaining between-male variation of eight song parameters in males sharing the same A and B song type.

Variable	Song type A (4 males compared)		Song type B (5 males compared)	
	$F_{3,65}$	p	$F_{4,107}$	p
DURATION	204.49	< 0.001	76.67	< 0.001
FMA	73.99	< 0.001	18.01	< 0.001
L25	13.42	< 0.001	83.96	< 0.001
M50	224.85	< 0.001	51.39	< 0.001
U75	69.25	< 0.001	76.70	< 0.001
MINF	8.6	< 0.001	11.88	< 0.001
MAXF	64.74	< 0.001	21.31	< 0.001
BANDWIDTH	21.79	< 0.001	18.99	< 0.001

We found that there were on average only 0.38 different song types per male within the studied population. 83% of males sung song types shared with at least one other male, and just over half of all song types were unique, i.e. sung by a single male (Table 3). Using the species richness concept, the estimated population repertoire size was only slightly higher than the real number of song types found in the population (21 ± 1.28

Table 3. Song type sharing within a local population of the Tawny Pipit. The first two columns indicate the number of males sharing a particular song type. Hence, one song type was shared by eight males, two song types were shared by five males and so on.

No of song types shared	No of males which shared particular type	Sum of males	Percentage	Cumulative Percentage
1	8	8	15.1	15.1
2	5	10	18.9	34.0
3	4	12	22.6	56.6
4	3	12	22.6	79.2
1	2	2	3.8	83.0
9	Unshared (i.e. sang by 1 male)	9	17.0	100.0
		53 males		100%

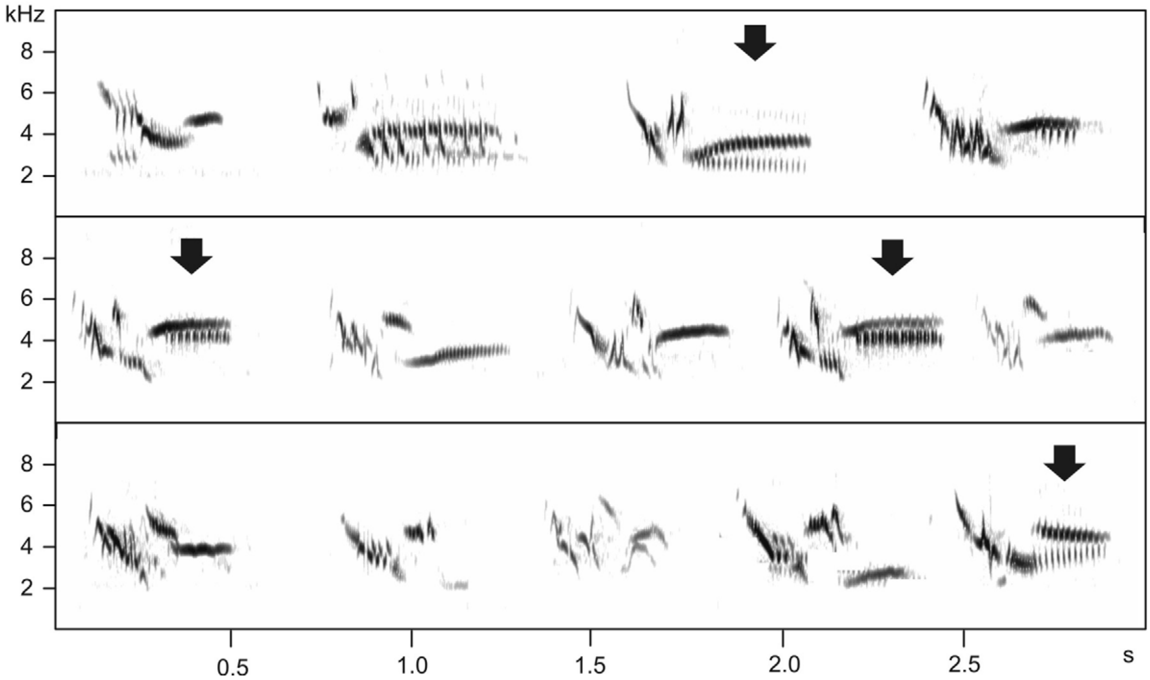

Fig. 1. Sonograms of typical Tawny Pipit song types from the studied population. Arrows indicate complex two-voices notes, i.e. consisting of two sounds produced simultaneously by different part of syrinx. Each song presented was devived from different males.

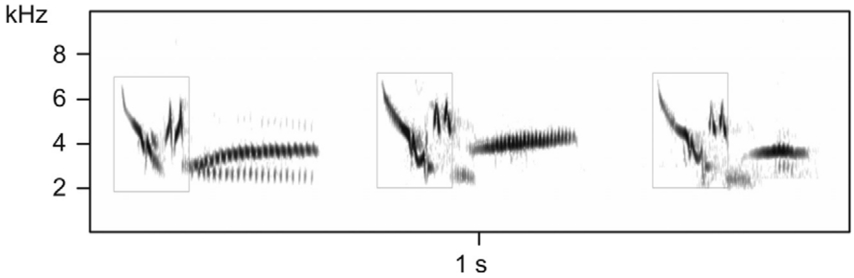

Fig. 2. Three different song types sung by different males. Each of these types has a similar initial part (indicated by rectangle), consisting of a whistle descending in frequency followed by a short double-note unite. Final parts of these song types were more or less different.

(mean ± SE)) song types; M(h) Goodness of Fit test $\chi^2 = 267.118$, df = 5, $p < 0.0001$). This result suggests that one should not expect to find many new song types in this population by recording a larger number of individuals.

For the most frequent song types (A and B, see Fig. 3 and 4), we measured the time and frequency parameters in order to test for differences between individuals. We selected for measurements between 8 and 31 songs per male, which had good and similar quality, assessed by visual inspection of the sonogram, and measured the amplitude of the signal. We found significant between-male differences, which concerned all of the measured song variables (Table 2). We also applied discriminant function analysis (DFA) to the song variables, to test whether individuals sharing the same song types could be correctly classified by within-song type variation. In the case of song type A, the DFA, based on the three song variables, showed 98.5% of correct assignments of song into males. For song type B, we had correct assignments in 89.8% of the cases.

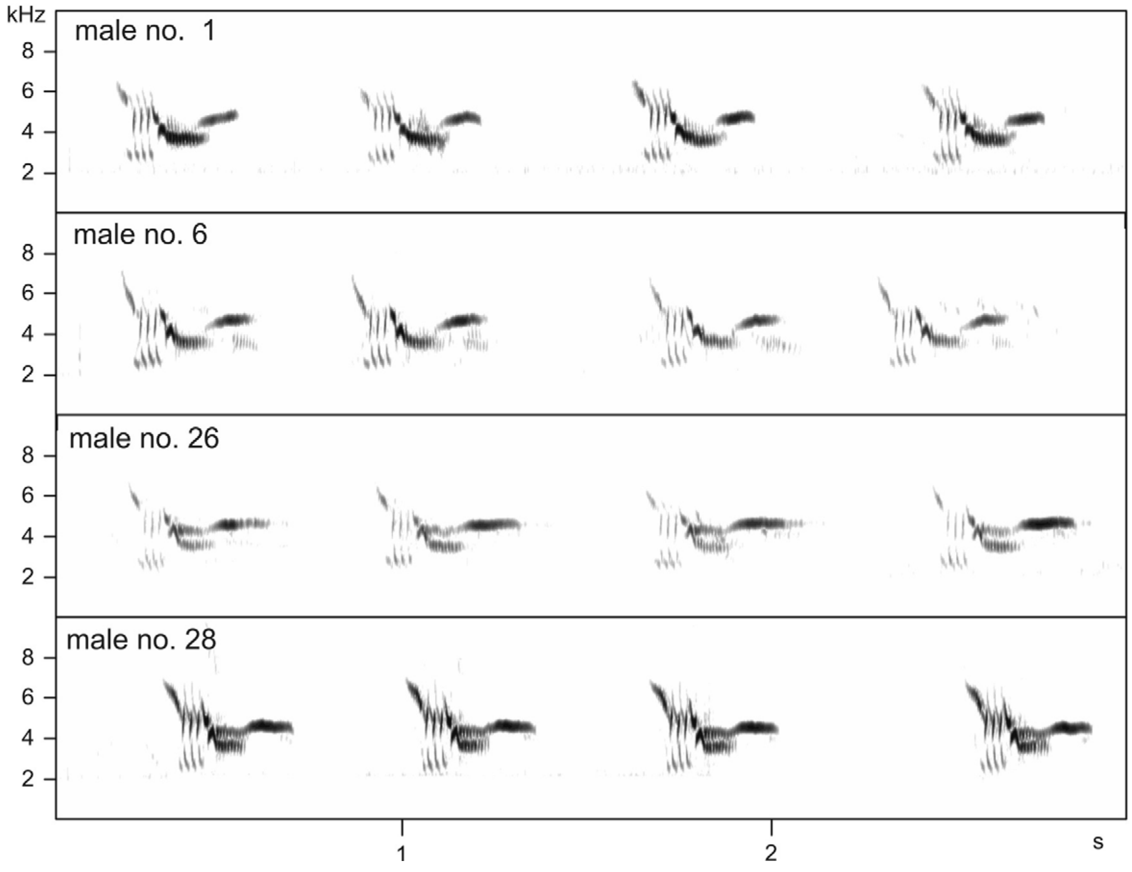

Fig. 3. Sonograms of one of the most frequent song types (A) illustrated by examples of songs from the repertoire of four different males.

DISCUSSION

The Tawny Pipit song is short and relatively simple. It resembles in structure the song of Berthelot's Pipit *Anthus berthelotii* and strikingly differs from the much longer and more complicated songs of the Tree *A. trivialis*, Meadow *A. pratensis*, Red-throated *A. cervinus*, Water *A. spinoletta* and Australasian *A. novaeseelandiae* Pipits (Bergmann & Helb 1982). We found that the Tawny Pipit performed his song with a highly varying rate, which suggests that song rate is the main channel of coding information about the singer's motivation or quality.

We found that the frequency parameters of the songs were not significantly correlated with their duration, which suggests that there is no species-specific auditory mechanism for species identity in frequency modulation across the song (compare Bradbury & Vehrencamp 1998, p. 580). Therefore we failed to find any species-specific song characteristics except for the duration and overall frequency pattern of the song.

Regardless of its short duration, the song of the Tawny Pipit consisted of 2–3 (maximum 5) units often with a very complex structure of short and tightly packed notes. The presence of consistent between-male differences, which also concerned males sharing the same song types, suggests that the song structure in this species may be important for individual recognition. The presence of complex acoustic structures within the songs, including two-voice syllables (Nowicki & Capranica 1986, Slabbekoorn & Smith 2000) also suggests its importance in individual recognition (Fandiňo-Mariňo & Vielliard 2004).

We found that each male within the studied population has a repertoire of a single song type, which suggests that there is no sexual selection acting towards an increased repertoire size in this species and that repertoire size is not important for communication in the Tawny Pipit. We also

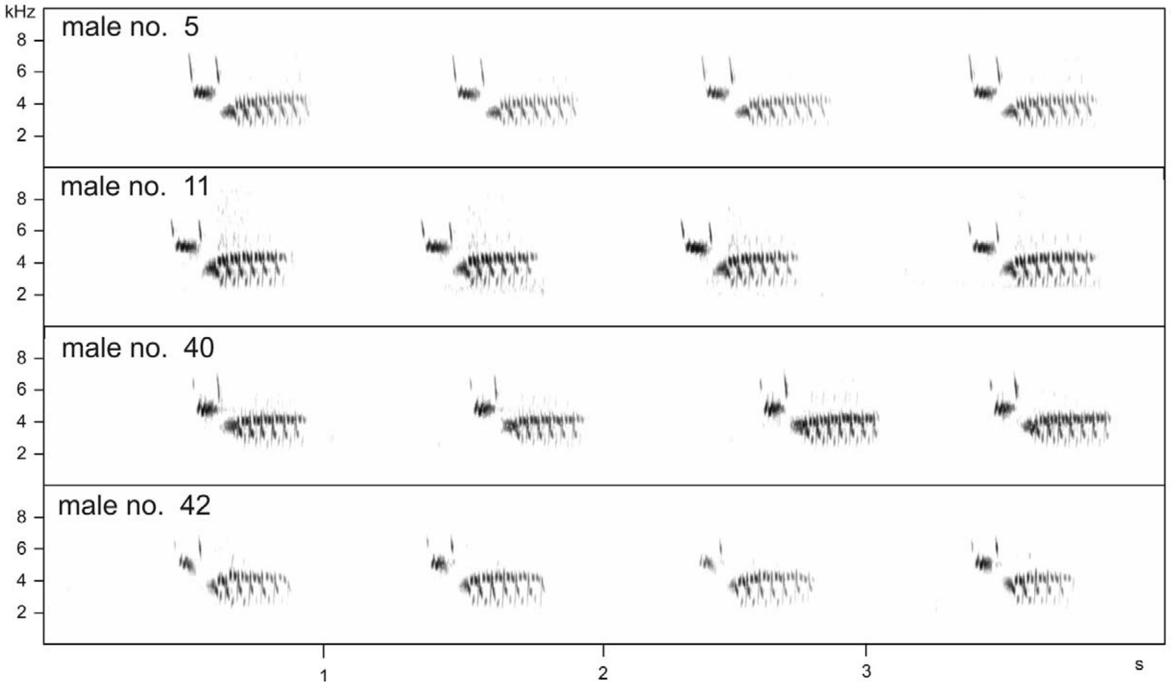

Fig. 4. Sonograms of one of the most frequent song types (B) illustrated by examples of songs from the repertoire of four different males.

found that the songs of different males were sometimes similar, others were completely different in structure (Fig. 1), and some song types partly shared unit(s) (Fig. 2). Finally some songs sung by different males should be assigned to the same type as they consisted of the same sequence of highly similar units (Fig. 3 and 4). However, shared song types in individual males were acoustically different because of slight but consistent variations in the timing or energy distribution within the song.

Our results on song sharing differ from the earlier findings of Neuschultz (1986), who found no song type sharing among 30 males recorded in Germany. He recorded males in a much smaller area (18 km^2) than we did (100 km^2), and in his study, population densities of Tawny Pipits were more than three times higher. One may link differences in song variation at the population level with differences in densities of territorial males. Trends found in *Cistothorus* wrens by Kroodsma et al. (2001) suggested that song repertoire size increased with population density, however in species with small repertoires the relationship between population density and song variation could be different. Larger distances between males in a fragmented population may promote an increase of song variation in such a species (Osiejuk et al. 2003). Moreover, the song sharing pattern may differ among neighbours and non-neighbours in relation to habitat fragmentation, as a result of the number of interactions among isolated and non-isolated individuals (Laiolo & Tella 2005). There is a need of further comparative research on the Tawny Pipit's song variation, particularly focussing on the populations' status (density, fragmentation, isolation etc.), as patterns of song variation found in nature differ strongly between species (e.g. Baker et al. 2006).

It is clear that some of the songs presented by Neuschultz (1986) belong to the same types as those described by us in Poland. For example, our most frequent song types A and B, were clearly present in the German population. Comparison of sonograms presented by Neuschultz (1986) also suggest that at least some of the song types described in Germany shared some units, however it is unclear how this author treated song types that were similar or almost identical in structure. It seems that he rather overestimated the population repertoire size. In this light, we consider song sharing is likely to be common in the Tawny Pipit and is probably not limited to local populations but occurs on a macrogeographical scale too. It is supported by many studies, as bird species with a single song type repertoire usually exhibit song sharing (review in Mundinger 1982).

To summarise, it seems that sharing song types or song parts may be important in this species and that song variation within the population may be less binary then was previously believed, as the similarity of the song types of different males may vary more continuously between 0 (different) and 1 (same song type). Songs of the Tawny Pipit are individually distinct and invariant, which suggests that they are important in individual recognition. Song rate is highly variable and is very likely to signal males' motivation or quality.

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STRESZCZENIE

[Charakterystyka śpiewu świergotka polnego]

Przeanalizowano śpiew 55 samców świergotka polnego nagranych w maju 2005 r. w Wielkopolsce w okolicach Koła. Samce śpiewały

z bardzo zróżnicowanym tempem od 4 do 28 piosenek na minutę, średnio 16.0 ± 1.35 (± SE). Piosenki świergotka polnego były bardzo krótkie, przeciętnie trwały około 0.5 sekundy i składały się z 2–3 (czasem do 5) podjednostek o paśmie częstotliwości od 2.7 do 5.3 kHz (Tab. 1). W oparciu o standardową analizę porównawczą sonogramów połączoną z analizą opartą o funkcje korelacyjne programów XBAT i Avisoft SASLab Pro, w badanej populacji udało się wyróżnić 20 różnych typów piosenek. Każdy samiec śpiewał wyłącznie jednym typem piosenki, a piosenki różnych samców różniły się od siebie w różnym stopniu. Niektóre samce posiadały piosenki niemalże identyczne, które różniły się wyłącznie drobnymi szczegółami struktury (Fig. 3 i 4). Niektóre piosenki samców były klasyfikowane jako należące do odrębnych typów, ale posiadały pewne wspólne podjednostki łatwe do zlokalizowania na sonogramach (Fig. 2). Wreszcie, część samców śpiewała typami które były całkowicie odmienne od wszystkich pozostałych w badanej populacji (Fig. 1). Aż 83% samców z badanej populacji śpiewało typem piosenki współdzielonym przez przynajmniej jednego innego osobnika, a 9 z 20 opisanych typów śpiewu było unikalnych, t.j. nie współdzielonych przez inne samce (Tab. 2). Mimo współdzielenia repertuarów piosenki poszczególnych samców posiadały cechy, które umożliwiają indywidualne rozpoznawanie się osobników (Tab. 3). Podsumowując, stwierdzono iż podstawowym sygnałem dotyczącym motywacji bądź jakości samców wydaje się być tempo śpiewu, podczas gdy struktura piosenki najprawdopodobniej odpowiada za identyfikację nadawcy. Po raz pierwszy wykazano u świergotka polnego współdzielenie repertuarów, choć możliwe jest, iż wcześniejsze badania nie wykazały tego zjawiska ze względu na odmienne podejście do analizy sonogramów.